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Distribution of Reaction Wood in Eastern Hemlock as a Function of its Terminal Growth

BY
FRANCOIS MERGEN

THERE ARE TWO distinct patterns in the growth of terminal leaders in the members of the *Coniferales* order. The pines, for example, have a terminal leader which assumes an upright, or orthotropic, orientation from the onset of cell elongation at the beginning of the growing season. These leaders exhibit negative geotropism and/or positive phototropism throughout the entire growing period. The terminal shoots on eastern hemlock trees, *Tsuga canadensis* (L.) Carr., on the other hand, droop at the beginning of the growing season and gradually turn upward as the season progresses. During this drooping period the leader is quite flexible and swings freely in the wind. This growth pattern is genetically fixed and is present throughout the life of the hemlock trees.

Eastern hemlock is an important timber species, and its wood is used for rough framing of houses, and for the manufacture of heavy shipping containers. One of the undesirable characteristics of this species is the high incidence of ring shake in the boles of living trees. These shakes are the result of rupturing between the cells and occur either along the boundary of two rings, or within the cells of the ring itself. These defects are concentric because the rupturing follows the outline of the rings. To the writer's knowledge, no detailed study has been made of the causes of these defects, although various theories have been advanced (Koehler, 1933).

This investigation considers some of the possible fundamental causes of these failures. It appeared reasonable to assume that these failures might be related to abnormal conditions in the growth pattern of hemlock trees. The growing pattern can affect the wood anatomy and cause the formation of irregular types of wood. Cursory observations in the field had shown that all the hemlock trees examined had zones of compression wood in the immediate area which surrounds the pith. It was postulated that the growth pattern of the leader might be the factor which causes these zones of compression wood, and that these zones might cause internal stresses which become the starting nuclei for the failures.

The present investigation was broken down into three distinct parts:

1. The growth pattern of the leader of hemlock trees was followed through one growing season, and a correlation was sought between leader growth and orientation, and type of wood produced.

The author is located at the Yale University Forestry Research Center, Valhalla, New York. Acknowledgment is made to L. E. Koerting for help with the field and laboratory work, and to Professor H. J. Lutz and P. F. Bourdeau for critical review of the manuscript.

2. The growth pattern of hemlock leaders was forced to follow an orthotropic pattern during one entire growing period and the wood which was subsequently produced was analyzed.

3. Sections of hemlock trees were subjected to alternating freezing and thawing cycles and to gentle bending during the frozen state to see whether or not minute ring "shakes" could be induced as a result of the differential shrinkage between compression wood and normal wood.

Review of Literature

Because of its drooping branches, the growth habit of eastern hemlock has been described as "exceedingly graceful" (Harlow and Harrar, 1941), and the horizontal branches as "graceful sprays of branchlets and twigs" (Frothingham, 1915). The terminal shoot is very flexible and droops away from the direction of prevailing winds (Frothingham, 1915). Harlow and Harrar (1941) suggested that the leader might be used with reservations as a "natural compass." For the pines, the current year's height growth is telescoped within the previous year's terminal bud (Doak, 1935), but for hemlock trees it originates during the current season from a growing point which is located about an inch back from the tip (Frothingham, 1915). This growth pattern is not only found in the hemlocks and other conifers of the temperate zones, but also in *Callitris cupressiformis*. This latter species is found in the tropics and the trees are growing throughout the entire year. The upper 2 feet of growth droop during the entire year and straighten from the base.

The wood of hemlock trees is brittle, and mature trees are commonly wind shaken. Frothingham (1915) described these shakes as the tearing apart of the cells between the annual rings as a result of the bending by the wind. These shakes are considered very undesirable by the lumber industry; in addition, peeled logs check badly during drying.

No reference to detailed observations of the leader growth in hemlock trees could be located. Curved leaders, however, do occur in spruce and pine. These bends are noticeable during the rapid elongation in the spring flush, and Gates (1928) explained these "nutations" (Gates' term) as a result of differential water pressure on different sides. A decrease in turgidity is caused by the sun and wind, which brings about a growth curve in the direction where the turgidity is lowest.

If the leader, or a branch, of a conifer tree is displaced from its normal orientation of growth, a special type of reaction wood is formed. In a leaning conifer, this wood is formed on the side where the cells are compressed, and therefore it is called compression wood (Büsgen and Münch, 1939). Münch (1938), and Hartmann (1932, 1943) postulated that this wood was of a regulatory nature and its function was to maintain the shape or orientation of the tree, the "static equilibrium," which was determined by its genotype. Reaction wood develops more longitudinally than normal wood and therefore causes the stem or branch to curve away from the region where it is formed. The stimulus which causes reaction wood in conifers was first thought of as being caused by the pressure which is applied to the cells during bending (Büsgen and Münch, 1929), but as of now, gravity is regarded as the main factor (Ewart and Mason-Jones, 1906; White, 1908, Sinnott, 1952, Scott and Preston, 1954). Wershing and Bailey (1942) noticed a relationship between auxin and reaction wood, which suggested a parallel between the distribution of the auxin and the reaction wood. Spurr and Hyvarinen (1954) reviewed the literature on the causes of compression wood initiation, and discussed them as a morphogenetic phenomena. Their conclusion was that ". . . . compression wood is formed indirectly as a counteractant to forces tending to deform a tree in any way," and that ". . . . it seems quite probable that auxin is the regulator which sets off the intracel-

lular reaction that causes formation of the anomaly."

The reaction wood differs from normal wood in anatomical, chemical, physical, and mechanical factors, and causes hypertrophy in trees (Hartmann, 1932, 1943). Because of its distinct macroscopic characteristics, such as its dark brown color, it has been called "rotholz," hard grain, and timber bind (Pillow, 1930).

Foresters have concentrated a great deal of attention on reaction wood because lumber with zones of reaction wood has inferior strength properties. Compression wood shrinks along the grain to a much greater extent than normal wood does, which results in splitting, bowing, and twisting along the grain (Pillow, 1930). The fibers are rounded and there are intercellular spaces between the individual cells; the fibers are also shorter than those from normal wood of the same tree (Dadswell and Wardrop, 1949). These properties cause internal stresses in the lumber when changes in moisture content take place.

Materials and Methods

Experiment 1. During the 1955 growing season, the growth pattern of the current year's terminal shoot was traced on 10 hemlock trees growing in a plantation. At the beginning of the studies these trees were 6 years old and had an average height of about 4.5 feet. A system of coordinates was used to plot the position of the leaders. The distance from the shoot to a line which was at the base of the current year's growth, and at right angles to the main axis of the tree was plotted at 1-inch intervals. A special device was built for this purpose (Figure 1 A). The measurements were made weekly and at a time of day when there was little wind movement. In addition to the shape of the leader, the general orientation was recorded.

The leaders were harvested during the spring of 1956 and sections were prepared for microscopic analysis. Cross sections were cut from the section at the base, and at 3-inch intervals up to the tip of the shoot. They were fixed in FAA, dehydrated, and stained with safranin to differentiate the compression wood. The leaders were marked on one side by cutting the bark, so that the precise orientation of the cross-sections could be maintained. The details of the cross sections were reproduced with the aid of a camera lucida at a magnification of $\times 20$.

Experiment 2. During the spring of 1956, 10 groups, with 3 hemlock trees in each group, were chosen in a plantation for their uniformity in rate of growth during the previous 2 growing seasons. Three types of treatments were applied at random to each group, namely: (a) no treatment; (b) the leader was maintained upright by tying it to a rigid stick, and (c) the leader was held upward by tying the growing tip to a string which was counterbalanced by a weight (Figure 2A, B, C). For treatment (b) a wooden post was driven in the ground next to the base of the tree and a rigid bamboo stick was tied to it. The tree was tied firmly to the post and the growing shoot was fastened to the stick with "Twistems." Due to the rapid growth, the ties had to be checked daily and adjusted to take care of internodal elongations which resulted in small bulges all along the shoot. For treatment (c) a wooden gallows was built to pull the leader upwards. A waxed fishing line was used and an Erlenmeyer flask, filled with water, served as ballast. Water was added to the flask as additional weight was needed.

At the end of the treatment period (October 16), the angle between the stem and the side branches was measured and a record of the total length, and of the diameter at the base, was also made. After the leaders were harvested, 1-inch segments were cut from the base, and at 5-inch intervals up the stem. They were fixed in FAA, and cross sections were cut on a sliding microtome. The microtome sections were stained in safranin and embedded in Permount.

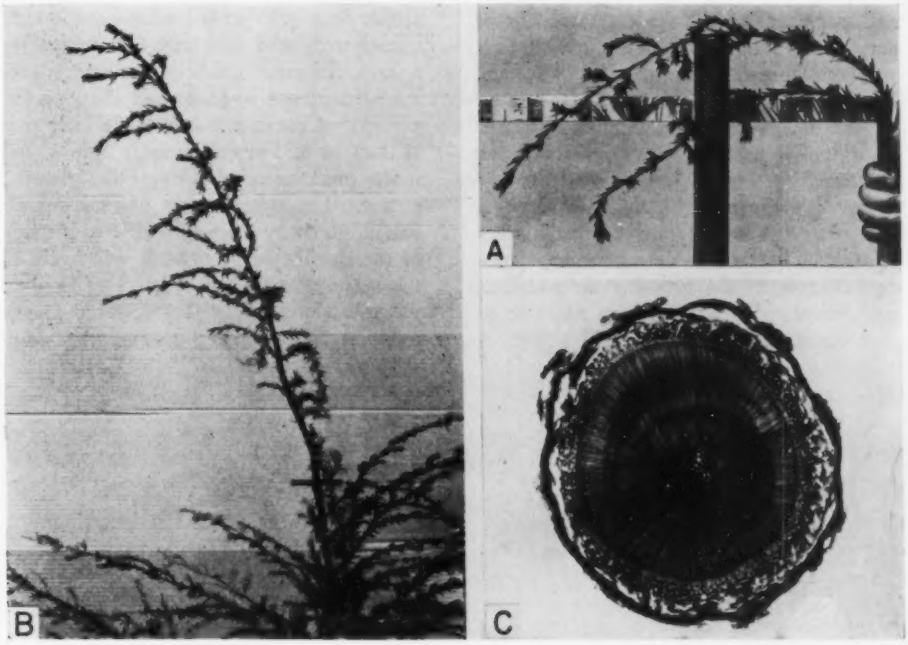

FIGURE 1. *A. Device used to measure the curvature of the terminal shoot. After each weekly measurement the data were plotted on graph paper to check for possible errors. B. Appearance of a leader before the onset of spring growth. The growth of the previous year did not straighten out completely, but there are several bends.C. Arrangement of the zones of compression wood in the lower portion of a leader.*

Experiment 3. During 1956 and 1957, the basal parts from seven 5-year-old hemlock trees were cut and placed immediately in a deep-freezer. Two of the stems were subjected to 136 alternating freezing and thawing cycles, while the remainder were subjected to 80 cycles. To thaw out the sections, they were placed in a basin of lukewarm water. During the thawing process, the stems were bent several times to simulate bending by the wind in nature. The sections were never allowed to dry but were always kept in a saturated atmosphere. As soon as the sections had thawed, they were returned to the freezer. At the end of the treating period, cross sections were cut with the aid of a sliding microtome. The pieces to be sectioned were clamped carefully in the chuck to minimize distortion, and the knife and wood were lubricated with water to prevent the wood from drying out. After the sections were examined and evaluated, they were dehydrated, stained and mounted in Permount for future reference.

Results

Experiment 1. At the beginning of the growing period the shoots were succulent and little lignification of the cell walls had taken place. The shoots were unable to maintain an erect or orthotropic growth, but were bending down under their own weight. During this stage, the orientation

and curvature of the leaders were almost parallel to those of the side branches which were growing from the past year's leader. No two trees followed exactly the same pattern during the straightening process. Four typical patterns of straightening are reproduced in Figure 3. The straightening appeared to be brought about by 2 types of mechanisms which are not directly interrelated. The first movement upward occurred close to the growing tip and was probably the direct result of a response to geotropism and heliotropism. This first response was quite varied between the individual trees, and was only of a temporary nature. In some instances it was most pronounced at the beginning of the growing period and decreased during the later part of the season. For tree number 7, however, it was pronounced all through the growing season. The straightening process was effected mostly by a bending close to the base of the current year's growth which caused the leader to turn upwards. This bending was accompanied by a stiffening of the cells. As the growing season progressed,

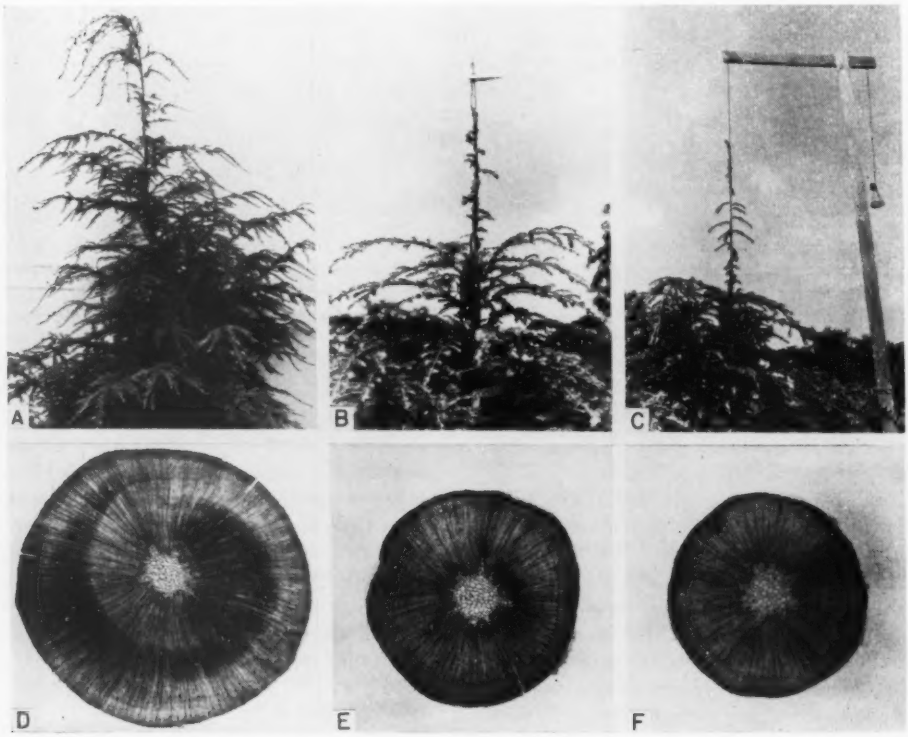

FIGURE 2. *A. Natural orientation of the terminal shoots (Control). B. Terminal shoot tied to a rigid stick. The clothespin was holding a sliding wire loop in place. This loop held the leader in place and was moved upwards as the elongation of the leader took place. C. Terminal shoot pulled upwards by a string. D. Transverse section through the base of the control. E. Transverse section through the base of a leader which was tied to the stick. Note the traumatic resin ducts in the upper part of the section. F. Transverse section through base of leader pulled up by a string. (Sections D, E, and F are all at the same magnification.)*

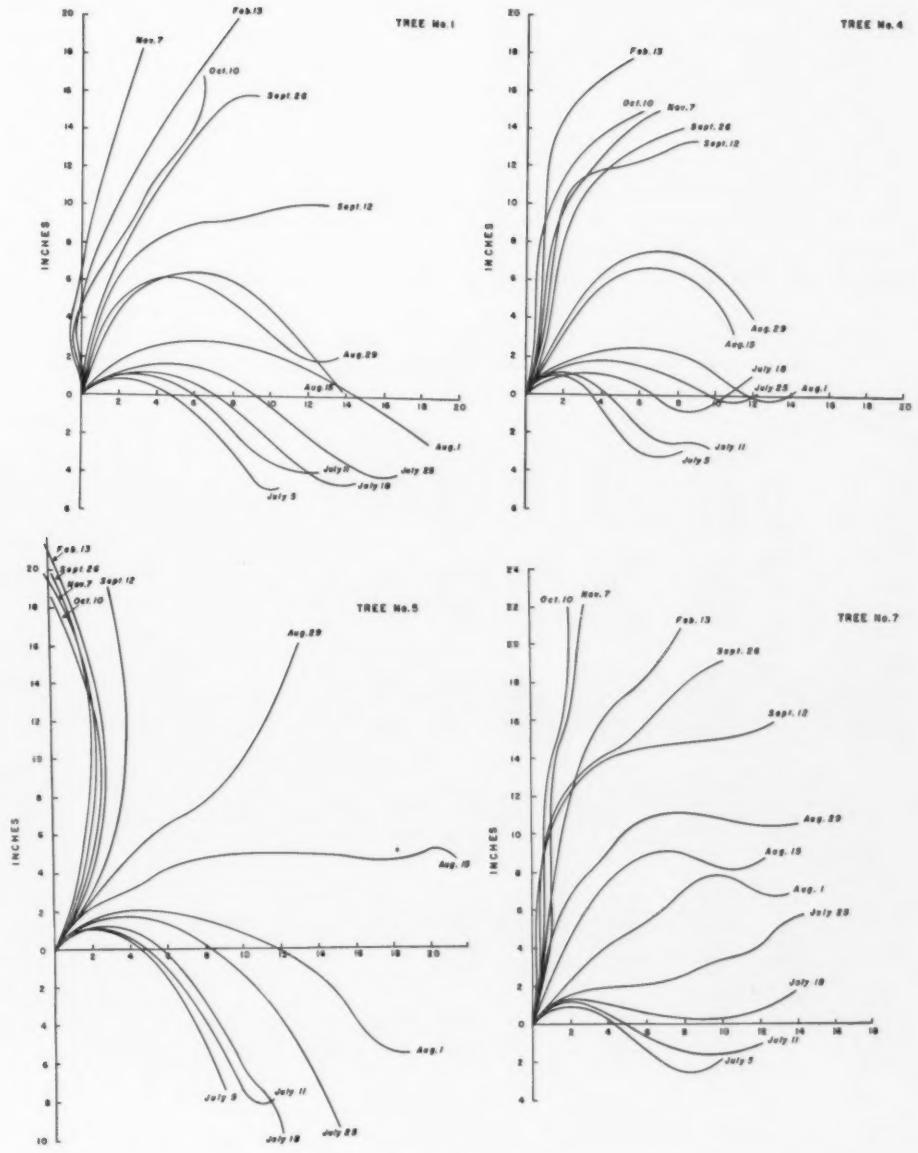

FIGURE 3. *Graphic presentation of the course of the straightening of the leaders in four of the test trees.*

this point of stiffening progressed up the stem. The effect of this stiffening process was very strong in some instances and caused an over-correction in the growth pattern. In these instances the leader had a curve at the end of the growing period which was opposite to the original one. This was especially pronounced in Tree No. 5. In no instance was the leader straight after the growing period, but showed various degrees of curvature (Figure 1B). A check was made on the leaders of several hundred trees which grew in the same plantation as the test trees, and none had a straight terminal. In most instances the curvatures for the previous years were oriented differently and did not have the same degree of curvature.

The orientation of the leaders (Fig. 4) did not follow a discernible pattern, and it changed somewhat during the growing season. For some trees, the change in orientation was gradual, while for other trees it was abrupt.

There were pronounced segments of compression wood in all the cross sections examined. It was especially pronounced in the bottom sections (Fig. 4). These areas of compression wood were not of the solid mass type, but they were composed of

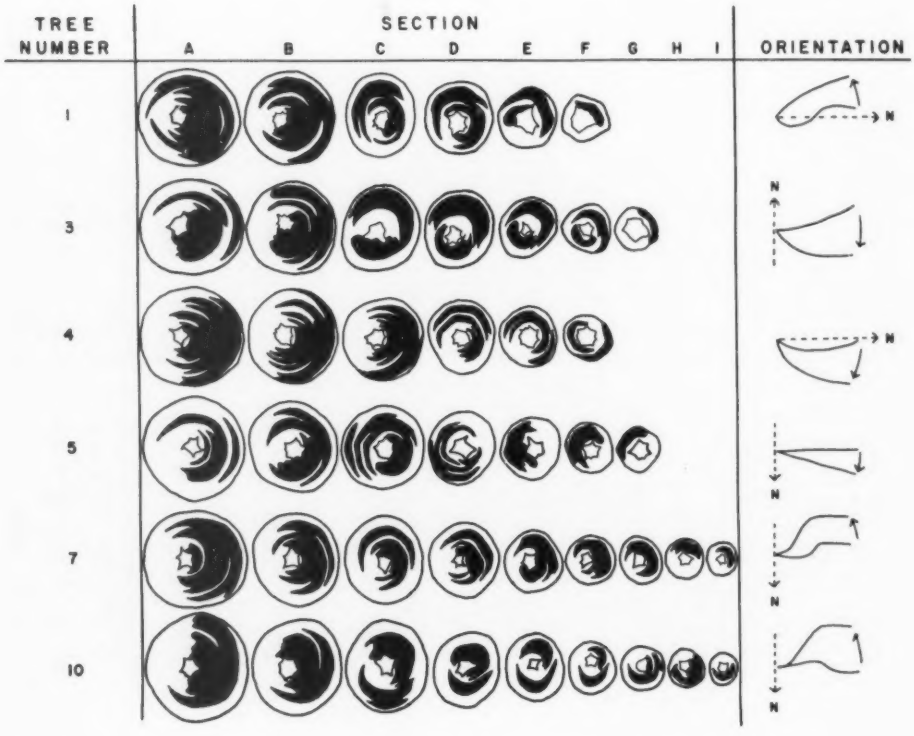

FIGURE 4. *Diagrammatic reproduction of transverse sections through the leaders showing the zones of compression wood. Section A is the cross section at the base of the leader. The orientation of the leader at the beginning of the growing period and at the end of the study is also given. The arrow indicates the direction of the change in orientation of the leader during the growing period.*

individual segments which reflected the orientation of the leader during the period when this reaction wood was laid down. As mentioned previously, Tree No. 5 had a curve at the end of the growing season which was in the opposite direction from that of the early part of the growing season. The reaction to this reversal is well illustrated by the change in the location of the compression wood. One must keep in mind that the areas closest to the pith were laid down first, and the thickening, or the radial growth, continued during the remainder of the growing season. The rate of change in orientation of the leader was also recorded by these zones of compression wood, e.g., in Tree No. 3 the change was abrupt, while in Tree No. 7, the change was gradual.

Experiment 2. By using a string to maintain an upright habit (Fig. 2C), straight leaders were obtained (Fig. 5). The leaders which were tied to a stick did not develop into perfectly straight stems, because the cell elongation which took place between the areas where they were tied to the stick caused small bends. In addition, it was necessary to fasten the leaders to the stick at a time when they were still succulent which prevented the placing of firm ties. The string method was most successful because the leaders were maintained in an upright position at all times, and the free-moving counterweight allowed the tree to be moved by the wind. It was of interest to note that both the longitudinal and radial growth were depressed in the leaders which were held in an upright condition (Table 1). The average angle of the side branches with the main stem was also much smaller than for the controls. Not only was the average angle smaller, but there was a definite increase in the angle of the controls when the side branches near the terminal were compared with those near the base. This average difference in angle was 32 degrees. For the treated leaders, the differences between the upper and lower side branches were random: in some instances there was a slight increase while in other instances there was a slight decrease.

TABLE 1. Average values for the length of the leader, the diameter (outside bark), and average angle between the branches and the main stem.

Treatment	Length	Diam. at base	Angle
	cm.	*cm.*	*degrees*
Control	61.2	.64	58
Stick	44.6	.38	87
String	48.4	.41	76

The microscopic examination of the cross sections of the leaders that were held upright by the string did not reveal any zones of compression wood. All the sections, including the basal one, were devoid of compression wood. The cross sections through the leaders which were held upright by tying them to a stick had small and poorly differentiated zones of com-

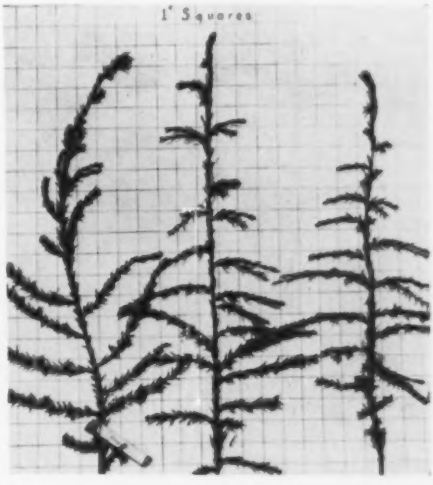

FIGURE 5. *Terminal shoots after treatment. Left—control; center—held up by string; right—tied to stick.*

pression wood in the areas close to the pith. This reaction wood was formed in the sections between the ties. Traumatic longitudinal resin ducts were also observed in several of these sections (Fig. 2 D, E, F).

Experiment 3. As a result of the alternating freezing and drying cycles, failures were induced in the stems (Fig. 6). These failures ran along a line in the springwood part of the ring in which they occurred. The failures extended for several centimeters up the stem. In one stem section there were two failures which were separated by a distance of 8 cm. They were not inter-connected and occurred on different sides of the stem.

Discussion

The question whether the compression wood which is produced as a result of the position of the leader is a factor contributing to the formation of ring shakes in older hemlock trees, was not completely answered. It was demonstrated, however, that ruptures between normal wood and reaction-wood cells can be produced in frozen hemlock stems as the result of simulated bending by wind. It had been observed that in hickory logs there is a relation between gelatinous fibers (tension wood) and internal stresses in the wood; and tension-wood fibers have been found to be associated with severe radial splitting in logs (Anonymous, 1956). It was not reported, however, whether these splits had occurred in living trees, or whether they were brought about by differential stresses during the drying process. Unless a living hemlock tree has a radial split in its stem, or another surface injury which extends through the bark, the cells within the bole are continually above the fiber saturation point. Therefore, these shakes do not occur as the result of stresses due to drying out, but must be caused by either external strains, or by internal stresses such as forces resulting from the differential shrinkage in response to freezing temperatures, or more likely by a combination of the two. Compression wood has a different coefficient of shrinkage due to freezing than normal wood, and, combined with bending stresses imposed by strong wind movements

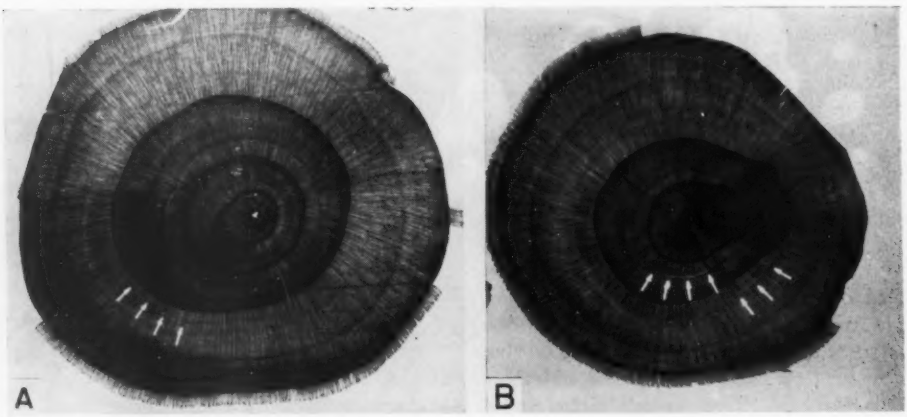

FIGURE 6. *Transverse section through the base of two 6-year old hemlock stems. The arrows indicate the failure (white line) which was brought about by the slight bending of the stem at a time when the stem was frozen.*

during a time when the wood is in a frozen state, these stresses might well be causative in starting minute shearing failures. As with other types of failures in the boles of living trees (Mergen, 1954), these first failures are microscopic in nature and enlarge as time passes. With large freezing facilities it should be possible to subject entire logs which have large zones of compression wood to alternating freezing and thawing cycles, and see whether or not failures between the rings can be brought about in this manner.

Of the species in which reaction wood was studied previously, the normal growth pattern of the trees had to be altered to produce it. Hemlock trees, on the other hand, produce this type of wood as part of their normal ontogeny. Their growth pattern appears to be dependent upon it, and its sensitivity determines to a large extent the shape of the bole during a considerable period of time. As mentioned previously, none of the leaders was perfectly straight at the end of the growing period but had various degrees of bends or curves. Moreover, the orientation of one year's bends showed no relation to the previous year's. As a result, unequal areas of radial growth have to be laid down in the various parts so the stems become cylindrical. This brings about unevenly distributed zones of compression wood. By selecting as parents hemlock trees which exhibit rapid lignification during the growing season and which produce straight leaders, it might be possible to breed hemlock trees that are less susceptible to ring shake.

From an evolutionary point of view it appears that at least in this height-growth characteristic, hemlock trees are not as advanced as the other members of the conifer order which have an orthotropic growth pattern from the beginning. Hemlock trees need to form reaction wood which is of a corrective nature, so that its crown is placed in a position where it can compete with other trees in the canopy. On the other hand, this flexible growth might have greater adaptive values. In hemlock trees, cell elongation and cell division take place during the active growing period, as compared to the pines where the current year's growth is laid down during the previous year's growing period. If during the growing period the terminal growing point of hemlock trees is damaged by an insect, or by mechanical means, hardly any amount of growth is lost, but a new growing point is formed immediately without leaving a noticeable bend in the leader. If the entire leader is cut off toward the latter part of summer, one of the side branches which is closest to the leader assumes dominance at once and leaves little trace of the damage. As a matter of fact it is very difficult at times to select the terminal leader during the growing season, and there appears to be a flexible, or a loose, pattern of apical dominance during the early part of the growing period. The arrangement of the branches during the summer months might also place the needles in a more favorable condition to carry out photosynthesis. Hemlock trees are classed as very tolerant and they can survive under dense overhead shade. The horizontal position of the branches, along with the linear arrangement of the needles lessens the amount of mutual shading between the needles, as compared to pines for example.

Observations of this study indicate that the formation of reaction wood is a very sensitive mechanism and is a graphic record of auxin activity, or auxin distribution, throughout the growing period of the shoot. A slight dislocation of the leader brings about a response in the formation of the compression wood. As in some of the previous studies, the compression wood was not only formed in the areas where the cells of the cambium were under direct compression, but it also formed on the interior side of the leader which was hanging downward.

The assumption that the curvature of the leader is in the direction of the prevailing wind is probably based on cursory observation On mountain tops, or in other areas

where there are strong prevailing winds during the growing season the direction of the curvature is probably determined by the wind.

It had been previously observed in conifers (Jacobs, 1939) that the bending movement by the wind brings about a stimulation of the cambium and as a result an increase in diameter growth. In these experiments, the larger diameter of the leaders subject to movement as compared to those which were prevented from moving, was well defined. If compared on a cross section basis, the average basal area of the control was about three times the size of those which were tied to the stick. The leader of the control was more than 30 percent longer than those of the treated ones. This possibly indicates that the swinging movements or the bending of a stem not only increases diameter growth but also stimulates height growth.

The cause of the increase in the angle between the side branches and the main stem is not known. It could have been brought about by purely mechanical means. The smaller angle could have become fixed in the control leaders if the cells in the side branches which were first formed started to lignify while the branches were hanging downward. For the treated ones, however, these side branches drooped from the beginning and lignification set in while they were in this position. On the other hand, in the controls, an auxin was probably produced as a result of this plagiotropic state which stimulated the formation of reaction wood and some of this auxin might have diffused to the side branches. Also, it is possible that these side branches on the controls assumed apical dominance for a short period of time. It has been reported that in the case where lateral buds develop on a stem that is bent, their side branches have a distinct tendency to suppress the terminal and they in turn assume dominance (Burns, 1942). In the treated ones, however, there was no stimulus to produce this auxin. From these observations it appears that hemlock trees would be very interesting test specimens to study auxin relationships and the biochemical aspects of reaction wood formation. Not only is it a very responsive species, but its normal ontogeny is opposite to that of the other conifers.

Summary

A relationship was sought between the shape of the terminal shoot of eastern hemlock trees and the type of wood produced. As a result of its peculiar height growth, irregular zones of compression wood are formed. It is postulated that these might be involved in the initiation of ring shakes.

The growth pattern of the terminal shoot was traced during one growing season and there was a strong correlation between the curvature and orientation of the leader and the reaction wood that was produced. By preventing the leaders from drooping during the growing season, no compression wood was formed. By subjecting green sections of hemlock stems to freezing and thawing cycles, and bending these sections gently during the frozen state, ruptures between normal wood and reaction-wood cells were produced. These minute failures which are brought about by differential internal stresses might be comparable to shearing failures which eventually enlarge to the size of the common ring shakes in the boles of living hemlock trees.

Literature Cited

Anonymous. 1956. Annual Report 1955. Southeastern Forest Experiment Station, For. Serv., U. S. Dept. Agric., Asheville, N. C. 80 pp.

Burns, G. P. 1942. Eccentric growth in the main stem of young white ash trees. Vt. Agric. Expt. Sta. Bull. 492: 19 pp.

Büsgen, M., and E. Münch. 1929. The structure and life of forest trees. Chapman and Hall, Ltd. London. XIX + 436 pp.

Dadswell, H. E., and A. B. Wardrop. 1949. What is reaction wood? Australian For. XIII: 22-33.

DOAK, C. C. 1935. Evolution of foliar types, dwarf shoots, and cone scales of *Pinus*. Univ. Ill. Bull. 32 (49): 106 pp.

EWART, A. J. and A. G. MASON-JONES. 1906. The formation of red wood in conifers. Ann. Bot. 20: 201-204.

FROTHINGHAM, E. H. 1915. The eastern hemlock. U. S. Dept. Agric. Bull. No. 152: 43 pp.

GATES, F. C. 1928. Nutation in *Pinus sylvestris*. Bot. Gaz. 85: 451-456.

HARLOW, W. M., and S. E. HARRAR. 1941. Textbook of dendrology. McGraw-Hill Book Company, Inc. XV + 542 pp.

HARTMANN, F. 1932. Untersuchungen über Ursachen und Gesetzmässigkeit excentrischen Dickenwachstums bei Nadel- und Laubbäumen. Forstwiss. Centralbl. 54: 497-517, 547-566, 581-590, 662-634.

————. 1943. Die Frage der Gleichgewichtsreaktion von Stamm und Wurzel heimischer Waldbäume. Biologia Generalis 17: 367-418.

JACOBS, M. R. 1939. A study of the effect of sway on trees. Comm. For. Bur. Bull. 26: 19 pp.

KOEHLER, A. 1933. A new hypothesis as to the cause of shakes and rift cracks in green timber. J. For. 31: 551-556.

MERGEN, F. 1954. Mechanical aspects of wind-breakage and wind-firmness. J. For. 52: 119-125.

MÜNCH, F. 1938. Untersuchungen über die Harmonie der Baumgestalt. Jahrb. f. wissenschaftliche Botanik 86: 581-673.

PILLOW, M. Y. 1930. Compression wood cause of bowing and twisting. Wood Working Industries, November 1930 Issue: 26-27.

SCOTT, D. R. M., and S. B. PRESTON. 1955. Development of compression wood in eastern white pine through the use of centrifugal force. For. Sci. 1: 178-182.

SINNOTT, E. W. 1952. Reaction wood and the regulation of tree form. Amer. Jour. Bot. 39: 69-78.

SPURR, S. H. and M. D. HYVÄRINEN. 1954. Compression wood in conifers as a morphogenetic phenomenon. The Bot. Rev. 20: 551-560.

WERSHING, H. F., and I. W. BAILEY. 1942. Seedlings as experimental material in the study of "redwood" in conifers. J. For. 40: 411-414.

WHITE, J. 1908. The formation of redwood in conifers. Proc. Roy. Soc. Victoria 20: 107-124.

Receptivity of Female Strobili of White Spruce

BY
HANS NIENSTAEDT

DETAILED INFORMATION on the period of pollen receptivity of the female flowers is essential in any tree breeding program. It is necessary to be able to recognize the developmental stage at which the flowers are receptive, to know how long this stage lasts, and to know how much it varies from one flower to another on the same tree and from tree to tree. Apparently no data on the receptivity of female spruce strobili have been published. Therefore, the study reported here on white spruce (*Picea glauca* (Moench) Voss) was made as part of the spruce improvement program recently started at the Lake States Forest Experiment Station.

Data regarding the period of pollen receptivity in other forest trees also are limited. In *Pinus* one study indicated that the period of maximum receptivity of an individual strobilus lasts 3 to 7 days (Cumming and Righter, 1948) and there apparently is a considerable variation in timing of the individual strobili on a tree. Duffield (1950) has pointed out that the opening of *Pseudotsuga* female buds is "more sudden and apparently more closely synchronized over a single tree than in *Pinus*"; even so, controlled pollination of a single tree requires several days to complete (Orr-Ewing, 1956). Four developmental stages are recognized in slash pine from the time the female strobili can first be seen until they have closed after pollination (Snow, *et al.*, 1943). The stages cover an average span of 15 days. A considerably longer period of receptivity has been described in *Castanea* (Nienstaedt, 1956).

Material and Methods

Six trees, about 30 years old and good seed producers, were selected for the study early in 1956. They are growing in a jack pine plantation on a very uniform site near Three Lakes in Oneida County, Wis. They are considerably taller than the surrounding pine, with the flowering portion of the crown fully exposed.

The primordia of the strobili in spruce are probably laid down in the early summer, and go through the winter as small conelets. The sexual buds are very difficult to distinguish in winter condition. The males are somewhat plumper and darker than the vegetative buds; the females are more slender and do not narrow abruptly at the base (Figs. 1 and 2). At this stage the males are globose and are 1 millimeter in diameter; the females are shaped like miniature cones 1 to 2 millimeters long.

By the end of April a slight swelling of these buds began to manifest itself; it was quite distinct by May 9. By May 18 the females were about 5/16 inch long and still tightly enclosed in the bud scales; the males were 3/16 inch in diameter and

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mostly tightly enclosed in the bud scales. A considerable enlargement had taken place by May 23, but most of the females were still completely enclosed. The majority of the males, however, were fully exposed, deep purple in color, and about ¼ inch in diameter.

The trees were bagged May 25 and 26 when the females were ½ to 1 inch long. At this time they were deep purple, and were breaking through the bud scales and turning into an erect position. The edges of the cone scales were beginning to turn back. The males were ⅜ to ½ inch long fully exposed, but no pollen shedding was observed on any of the sample trees or on any of a number of adjacent trees that were examined. The strobili were covered with bags of viscose casing of the type commonly used in the pollination of southern pine. This bag type has been found unsatisfactory for spruce if used alone, as it may cause overheating.[1] They were therefore cov-

[1]Personal communication from Mark Holst, Petawawa Forest Experiment Station, Chalk River, Ontario, Canada.

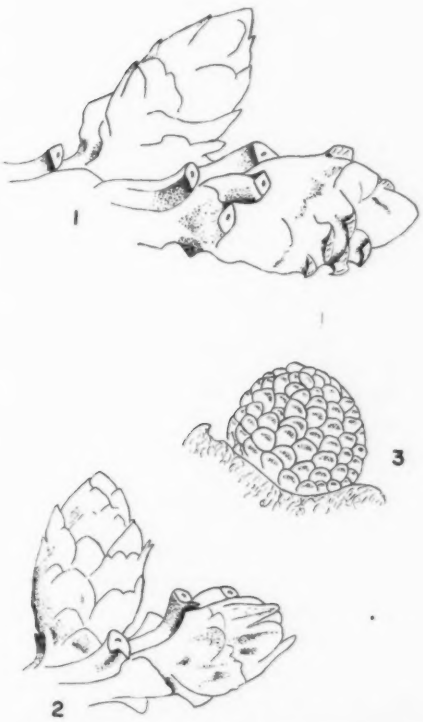

FIGURE 1. *Male buds of white spruce,* Picea glauca, *in winter condition, March 20, 1956. 1 and 2: male buds on the left, vegetative buds on the right. The male buds are short and broad with little or no curling of the edges of the budscales. They are dark brown; vegetative buds are tan-brown. 3: male strobilus with budscales removed. The dotted areas indicate a characteristic concentration of chlorophyl.*

FIGURE 2. *Female buds of white spruce in winter condition, March 20, 1956. 1 and 2: female buds on the left, vegetative buds on the right. The female buds are narrower, somewhat longer, and more pointed than the vegetative buds. 3: female strobilus with budscales removed. 4: vegetative growing point, with needle primordia in characteristic spiral arrangement.*

ered with additional kraft paper bags. The isolation was quite successful—in no case did filled seed develop in unpollinated bags.

Pollinations were made each day from May 28 to 31 and on June 1 and 3. A mixture of equal parts of pollen from the study trees was used. In one case, however, pollen from another tree had to be substituted. On each date three bags on each tree were pollinated; in addition three bags on each tree were left unpollinated as a control on the bagging, and three unbagged branches were tagged to make comparison with open pollinations possible. The pollination bags were removed June 13.

The following data were collected: (1) Number of cones per bag at the time of bagging, debagging, and harvest; (2) total number of seeds per bag; (3) number cleaned seeds per bag; and (4) total weight of cleaned seeds per bag.

TABLE 1. Pollen receptivity of female strobili on six white spruce trees.

Period of pollination	Percent bags with cones averaging— 15 seeds or less	More than 15 seeds
5/28 to 5/30	35.8	64.2
5/31 and 6/1	43.7	56.3
6/3	100.0	-----

Results and Discussion

Table 1 shows the results of pollination on all six trees. The general trend is clear: the pollinations were effective over the first 5 days but somewhat better the beginning 3 than the last 2. Pollinations on the seventh day were entirely ineffective.

There was considerable variation between trees (Fig. 3). Trees 1 and 4

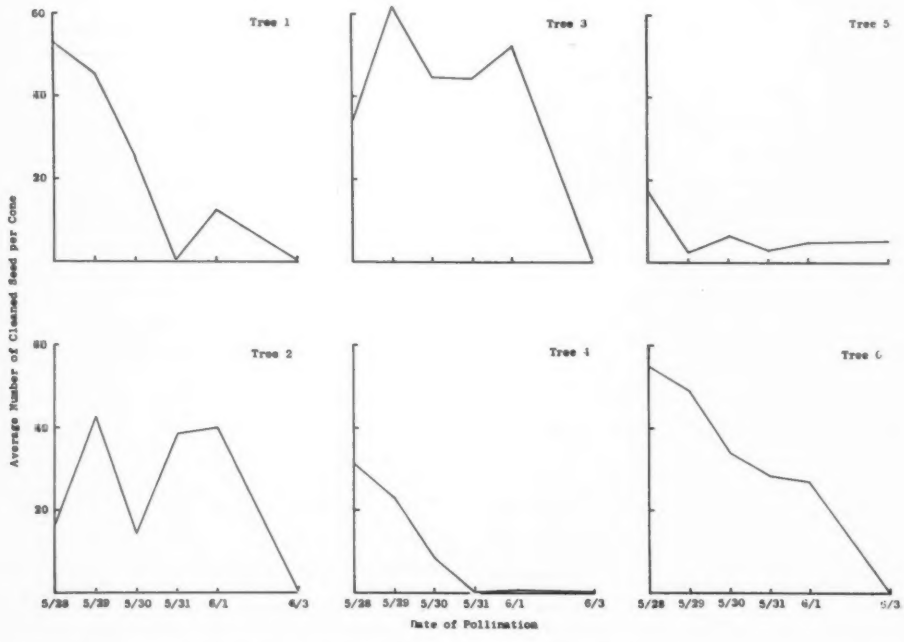

FIGURE 3. *Pollen receptivity of six white spruce trees on specified dates.*

showed a sharp decrease in yield the second day and reached close to zero values on the fourth day. Tree 1 yielded some seed from the fifth day's pollination but not nearly as much as on the first 3 days. Apparently the strobili developed earlier in this tree than in the others; it was bagged on May 26 and at that time the females were completely open and may have been receptive (Fig. 4). Very likely tree 4 also was early compared with the other trees.

Tree 3 yielded less seed from the first day's pollination than from the second, third, fourth, and fifth, as did tree 2 except for the third pollination, whose low value is probably due to some extraneous factor beyond the control of the experiment. These trees probably did not reach full receptivity until May 29. On both, the female strobili remained completely open on the third day when many of the cones were beginning to close on the other trees. The results with tree 5 are uniformly poor and may possibly indicate the occurrence of partly sterile white spruce trees.

The time of flowering of male and female strobili is compared in Table 2.

Although the peaks of the graphs (Fig. 3) may not be altogether trustworthy as indications of the dates of maximum receptivity, it seems safe to conclude from Table 2 that pollinations performed between the time of the first and the maximum pollen shedding may be expected to yield good results. This information has considerable practical value: pollen shedding is a readily observed stage in the development of the strobili and may be easily used in determining the correct time for pollination.

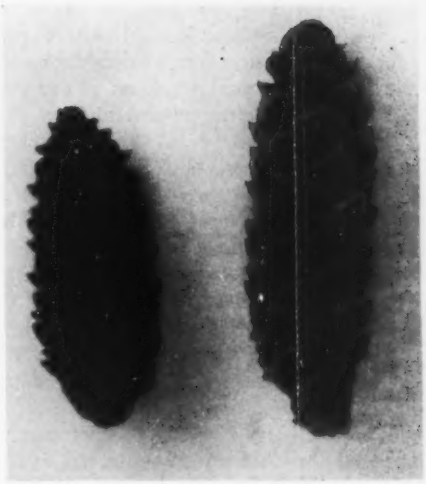

FIGURE 4. *Pollen-receptive female flowers from two different trees of white spruce, May 28, 1956. The larger flower is about ¾ inch long.*

TABLE 2. Flowering dates for male and female strobili of white spruce in northeastern Wisconsin, 1956.

Tree No.	Date of most effective pollination	Date of first pollen shedding	Date of maximum pollen shedding
1	5/28	5/28	5/30
2	5/29	5/28	5/29 & 5/30
3	5/29	5/29	5/30 (poor)
4	5/28	5/28	5/29 & 5/30
5	5/28	5/28	5/30 & 5/31
6	5/28	5/29	5/30 & 5/31

The over-all results of the controlled pollination were good. The 555 cones pollinated in 86 bags on the first 5 days of pollination yielded a total of 15,704 filled seeds or 28.3 seeds per cone. This compares favorably with the yields obtained by Tripp and Hedlin (1956) on open-pollinated trees. They consider a yield of 25 percent (23 seeds per cone) of the potential seed per cone to be about a maximum in a good seed year.

The yield of seeds per cone in different bags showed considerable variation, as was expected. This is probably due partly to differences in the development of the female strobili. Even so, the results indicate that little would be gained by confining pollination at any one time to the fully receptive strobili. It is doubtful that the additional

labor involved would be justified by a possible slight increase in yield of seeds per cone. In this connection it should be noted that the experimental procedure in this test fails to determine the earliest stage of receptivity. We cannot rule out the possibility that pollen once introduced in the bags may cause pollination over several days. Delayed pollination of this type, however, probably was at a minimum in the 1956 season, during which repeated wetting of the bags very likely caused the pollen to cake.

The loss of open-pollinated cones between the time of bagging and the time of harvest was considerable, as may be seen in Table 3.

The total loss (including cones partly damaged by insects) of open-pollinated cones was 83.0 percent, whereas only 22.4 percent of the bagged strobili were lost. This heavier loss of open-pollinated cones was in part due to a greater amount of insect damage as evidenced by the number of cones partly damaged by insects; these constituted 3.3 percent of the total harvest of bagged flowers but 56.5 percent of the harvest of open-pollinated cones. Apparently even a short period of bagging offers considerable protection against insect attack.

The average number of seeds per cone for open-pollinated flowers was only 6.0 (compared to 28.3 for hand pollinations). This low yield and the considerable portion of the open-pollinated cones lost are probably the result of unfavorable conditions for natural pollination during the period of maximum pollen flight, May 29-31. A heavy shower in the late morning on May 29 and intermittent showers on May 30 and particularly on May 31 made conditions for pollination very unfavorable. Thus the poor weather during the pollination season practically eliminated the potentially heavy seed crop.

Some additional observations were made during the study. Bagged but unpollinated strobili tended to remain open somewhat longer than unbagged flowers. Lack of pollination probably explains this in part; it is generally recognized that sterile flowers remain in bloom longer than fertile pollinated ones. It also appeared that strobili close to the top of the crown remained open longer than the lower ones.

In conclusion it should be recalled that this study was limited to only one growing season. Some variation in the length of the period of receptivity probably can be expected from year to year depending on the weather conditions.

Summary

1. The period of receptivity of the female strobili of six white spruce trees growing in northeastern Wisconsin was studied.

2. The results indicate that bagged white spruce strobili are receptive during a

TABLE 3. Cone losses between the time of bagging and harvest.

Time of count	Controlled pollinations[1]		Open pollinations	
	No. of cones	*Percent loss*	*No. of cones*	*Percent loss*
Bagging	715	-----	-----	-----
Debagging	657	8.1	118	-----
Total harvest	574	19.7	46	61.0
Good cones harvested	555	22.4	20	83.0
Insect-damaged cones harvested	19	3.3[2]	26	56.5[2]

[1]Only the cones from the first five pollinations are included.

[2]In percent of total harvest.

period of 3 to 5 days.

3. There is some variation from tree to tree. On a single tree, however, the development is fairly well synchronized, so that little can be gained by pollinating only fully receptive strobili over a period of days.

4. Pollen shedding — an easily recognized stage of development — appears to coincide fairly well with female receptivity and can be used to advantage in timing controlled pollinations.

5. The results of the experiment emphasize that weather conditions during the period of pollination may be very important in determining the size of the natural seed crop. Another important limiting factor is insect pests.

Literature Cited

CUMMING, W. C., and RIGHTER, F. I. 1948. Methods used to control pollination of pines in the Sierra Nevada of California. U. S. Dept. Agric. Cir. 792, 18 pp., illus.

DUFFIELD, JOHN W. 1950. Techniques and possibilities for Douglas-fir breeding. J. For. 28: 41–45.

NIENSTAEDT, HANS. 1956. Receptivity of the pistillate flowers and pollen germination tests in genus *Castanea*. Z. Forstgenetik und Forstpflanzenzüchtung 5 (2): 40-45, illus.

ORR-EWING, A. L. 1956. Controlled pollination techniques for the Douglas fir. For. Sci. 2: 251-257, illus.

SNOW, A. G., DORMAN, K. W., and SCHOPMEYER, C. S. 1943. Developmental stages of female strobili in slash pine. J. For. 41: 922-923, illus.

TRIPP, HOWARD A., and HEDLIN, ALAN F. 1956. An ecological study and damage appraisal of white spruce cone insects. For. Chron. 32: 400-410, illus.

Forthcoming Meetings

July 21 - 25	Geneva	FAO/ECE Study Group on the Handling and Transport of Timber in Mountainous Regions
July 22 - 25	Rome	Executive Committee of the International Poplar Commission
July 28 - Aug. 1	Geneva	FAO/ECE Study Group on the Application of Machinery to Forest Work
July - Aug. (6 weeks)	Denmark	FAO Training Center on Production, Certification, and Distribution of Tree Seed
Aug. 20 - 31	Guatemala	Latin American Forestry Commission—6th Session
Sept.	Austria	EFC Working Party on Torrent Control and Avalanches—4th Session
Sept. 25 - Oct. 10	Yugoslavia and Greece	International Chestnut Commission—4th Session
Oct. 18 - Nov. 1	Iraq	Near East Forestry Commission—2nd Session

Rooting Cuttings of White Pine

BY
R. F. PATTON
A. J. RIKER

VEGETATIVE PROPAGATION is an important tool for forest tree improvement. The rooting of white pine cuttings has been a part of the 20-year-old project in Wisconsin on the development of blister rust resistance in eastern white pine (*Pinus strobus* L.). Cuttings from 4- to 6-year old white pine trees form roots easily, but those from older trees root with more difficulty. Because selections for blister rust resistance generally must be from among older trees, emphasis has been focused on rooting cuttings from older trees. Heimburger (1956) suggested the use of rooted cuttings of resistant selections as interim planting stock until seed orchards could be developed. Thomas and Riker (1950) reported on basic literature and progress on rooting cuttings of white pine. An extensive literature review appears in Mergen's (1955a) report on vegetative propagation of slash pine.

The present paper reports results from additional investigations on rooting of white pine cuttings concerned with various chemical and physical treatments of cuttings and influences of the parent stock.

Methods

Cutting beds, 4 x 12 ft., established outdoors at the Griffith State Nursery, Wisconsin Rapids, Wisconsin, for previous experiments, were supplemented by others in 1953. Frames of wood or of concrete blocks were partially sunk into the ground. Soil was excavated and replaced with a layer of coarse gravel for drainage, and above this by an 8- to 10-inch layer of builder's sand. Two of 6 beds were equipped with soil heating cables, and with thermostats. Sand temperature was held at about 80° F. Wind screens 18 in. high were erected around each frame. To prevent desiccation the open beds were watered automatically by sprinklers controlled through solenoid valves by an electric clock and an interval timer (Thomas and Riker, 1950). For the first few seasons the spray cycle was for 1-2 minutes every 15 minutes at the beginning, and reduced toward the end of the season to a spray of 30 seconds, and later, to 15 seconds duration. Beginning with the 1954 season, sprinklers operated for 1 to 2 minutes on a 1-hour cycle. When the longer spray interval was used, half-shade was provided the cuttings by laying lengths of snow fencing across the tops of the wind screens.

The authors are respectively Assistant Professor and Professor, Department of Plant Pathology, University of Wisconsin, Madison. This work was supported in part by the Wisconsin Conservation Department and the U. S. Department of Agriculture. Most of it was done at the Griffith State Forestry Nursery, Wisconsin Rapids, Wisconsin, where W. H. Brener, Asst. Supt. of Forests and Parks kindly provided land and facilities. Prof. J. E. Thomas, Oklahoma A. & M. College, did much of the earlier work and established the 1949 series of cuttings. Paper approved for publication by the Director of the Wisconsin Agricultural Experiment Station.

All cuttings were of the most recent season's growth of 12- to 80-year-old white pines growing near Wisconsin Rapids, Wisconsin. Controls for judging rooting conditions were cuttings from 4-year-old (2-2) seedling transplants from the Griffith State Forestry Nursery, Wisconsin Rapids. Experimental controls for judging effectiveness of treatments included cuttings from the same source as test material.

Prior to 1954, 90 cuttings were used per treatment, divided equally among 3 cutting beds. One of the 3 replicates had bottom heat in the sand provided by the soil heating cable. Beginning with the 1954 series, the spacing between cuttings within rows was widened from approximately 1½ in. to 2½ in. and between rows from 2 inches to 4 inches to provide for better aeration so as to decrease the rotting of needles at the soil surface. The total number of cuttings per treatment was thus reduced to 60, with 20 in each bed.

In previous work (Thomas and Riker, 1950) treatment of young-tree cuttings with indole-butyric acid (IBA), as a soak or dip, produced better rooting results than untreated controls, with rooting up to 15-20 percent common after certain growth regulator treatments. In the present investigations further increases were sought through supplementary treatments with other materials. The standard treatment used was a soak of the basal inch of the cuttings in a solution of 50 p.p.m. IBA in water (IBA-50) for 24 hours. Time and concentration may be adjusted if necessary to give equivalent results; for example, IBA-100 for 12 hours is approximately equal in effect to IBA-50 for 24 hours. Another method of application used was to dip the basal inch for one second into a solution of IBA at 10 mg./ml. in 50 percent ethyl alcohol. Talc-dust mixtures also were sometimes used as dips. One contained as the active ingredient 0.3 percent IBA, while the active ingredient of another mixture ("Floramon C"—manufactured by Danydea A/S, Denmark) was unknown.

A standard procedure in handling the cuttings was followed for most of the tests during the period 1949 to 1956. Cuttings were usually made in August or early September. They were treated immediately, then placed in the cutting beds and watered until freezing weather prohibited use of the automatic sprinkling system. Little or no change in appearance of the bases or tops of the cuttings was evident at this time As necessary the cuttings were sprayed with suspensions of ferbam, thiram, or captan, to prevent snow mold. They were mulched over winter with a layer of marsh hay. Early in the spring (late April or first part of May) the mulch was removed and the automatic sprinkling resumed. Cuttings were removed for examination in late July or early August.

Experimental Results

Controls. Rooting among control cuttings of 4-year-old nursery transplants varied considerably from year to year which indicated the type of "rooting year" (Table 1). If the controls were good, other tests were fair; if the controls were poor, other tests were very poor. Thus the general level of rooting of the controls served rather like an index of rooting conditions, including environmental influences both before and after the cuttings were made.

Treatments given the controls always included a 24-hour soak in indole-butyric acid at 50 p.p.m. (IBA-50) as a standard. The efficacy of a given treatment varied from year to year, and sometimes also, on different lots of cuttings in the same year. Treatment with IBA generally but not always gave better rooting than no treatment. One year an IBA soak was much better than an IBA dip, whereas another year the reverse was true. Witness, for example, the variation obtained in 1953 with IBA soak and dip treatments with cuttings taken only 2 weeks apart (Table 1).

Treatments with carbohydrate and nitrogen sources. During a 7-year period, over 18,000 cuttings from white pines 12 to

TABLE 1. Rooting of control cuttings from 2-2 white pine transplants during the period 1950-1956.

Cutting year	Date of cuttings	Treatment	Total cuttings	Cuttings rooted	
			No.	*No.*	*Percent*
1950	Aug. 11, 1949	IBA-100, 12 hr. soak	90	30	33
	Aug. 11, 1949	None	90	24	27
1951	July 28, 1950	IBA-50, 24 hr. soak	90	64	71
	July 28, 1950	None	90	53	60
	July 28, 1950	Basal slits	90	45	50
	July 28, 1950	Water soak	90	45	50
	Aug. 24, 1950	IBA dip	90	47	52
1952	Aug. 9, 1951	IBA-50, 24 hr. soak	90	73	81
	Aug. 9, 1951	None	90	36	40
	Aug. 9, 1951	Water soak	90	25	28
	Aug. 24, 1951	IBA-50, 24 hr. soak	89	62	70
	Aug. 24, 1951	None	90	30	33
1953	Aug. 14, 1952	IBA dip	90	55	61
	Aug. 14, 1952	IBA-50, 24 hr. soak	90	54	60
	Aug. 14, 1952	None	90	43	48
	Sept. 3, 1952	IBA-50, 24 hr. soak	90	65	72
	Sept. 3, 1952	IBA dip	90	30	33
1954	Aug. 19, 1953[1]	IBA-50, 24 hr. soak	90	63	70
	Aug. 19, 1953	IBA-50, 24 hr. soak	90	58	65
	Aug. 19, 1953	IBA dip	90	64	71
	Aug. 19, 1953	IBA dip	90	52	58
	Aug. 19, 1953	None	90	35	39
	Aug. 19, 1953	None	90	30	33
	Sept. 14, 1953	Floramon dust	90	52	58
	Sept. 14, 1953	IBA-75, 18 hr. soak	90	39	43
	Aug. 19, 1953[1]	IBA-50, 24 hr. soak	90	37	41
	Aug. 19, 1953	IBA dip	90	36	40
	Aug. 19, 1953	None	90	15	17
1955	Aug. 16, 1954	IBA-50, 24 hr. soak	60	57	95
	Aug. 16, 1954	IBA dip	60	52	87
	Aug. 16, 1954	0.3% IBA in talc	60	44	73
	Aug. 16, 1954	Floramon dust	60	37	62
	Aug. 16, 1954	None	60	34	57
1956	Aug. 22, 1955	0.3% IBA in talc	60	29	48
	Aug. 22, 1955	IBA dip	60	22	37
	Aug. 22, 1955	IBA-50 soak	60	17	28
	Aug. 22, 1955	None	60	8	13
	Feb. 2, 1956	IBA-50, 24 hr. soak	60	24	40
	Feb. 2, 1956	IBA dip	60	22	37
	Feb. 2, 1956	Floramon dust	60	11	18
	Feb. 2, 1956	IBA-50 soak + Floramon dust	60	10	17
	Apr. 24, 1956	IBA-50, 24 hr. soak	60	29	48
	Apr. 24, 1956	IBA-50 soak + Floramon dust	60	22	37
	Apr. 24, 1956	Floramon dust	60	11	18
	Apr. 24, 1956	0.3% IBA in talc	60	3	5

[1]Cuttings in the first 8 treatments were rooted in sand; those in the last 3 treatments were rooted in sand—compost mixtures.

40 years old were treated with basal soaks in solutions of various sugars or other carbohydrates at different concentrations alone and in combination with a variety of nitrogen sources and concentrations (Table 2). Cuttings were obtained during this period from a plantation which was 12 years old at the beginning of the trials. In addition, a few of the treatments were also applied at various times to cuttings from trees approximately 30-40 years of age.

In 1950 the rooting percentages of

groups treated with both sugar and a nitrogen source ranged slightly higher than groups treated with sugar only, but rooting of experimental controls was similar to both groups.

Basal soaks and vacuum treatments in 1951 gave extremely erratic results. No consistent relationships appeared with regard to carbohydrate source, concentration, vacuum pressure, or period of exposure. Though the highest rooting percentages in the treated cuttings were well above the controls, the lack of any consistent pattern was apparent. For example, the highest rooting percentage of all (62 percent) was in one group treated merely by a basal soak for 24 hours in a solution of 1 percent dextrin and 50 p.p.m. IBA. Another group of 90 cuttings treated with 4 percent dextrin under vacuum of 400 mm. of mercury for 30 minutes followed by a concentrated IBA dip yielded 61 percent rooted cuttings.

In the 1952 trials 9 different treatments gave rooting percentages that were from 2 to 21 percent greater than the highest of the controls. Again the only pattern was that the nitrogen sources at the 2 highest concentrations were toxic and usually inhibited rooting.

In the more extensive trials with nitrogen sources in 1953 most of the rooting percentages ranged from minimums of 1 to 4 to maximums of 3 to 13 percent. The urea treatments, however, gave 10, 21, and 14 percent rooting from low to high concentrations, respectively. It appeared to stand alone above all the other substances used.

TABLE 2. Summary of treatments with and without carbohydrate and nitrogen sources to induce rooting of cuttings from 12- to 40-year-old trees.

Year	Type of treatment with carbohydrate and nitrogen	No. of treatments	Range of rooting	Treatment without carbohydrate or nitrogen soaks	No. of treatments	Range of rooting
			Percent			*Percent*
1950	Dextrose, levulose, sucrose, lactose, dextrin, soluble starch, glycerin[1]	14	1-21	IBA dip, IBA-50, NAA	3	4-21
	Sucrose + urea, sucrose + NH_4SO_4 —with and without IBA dip	6	11-24			
1951	Levulose—basal soaks or partial vacuum[2]	14	4-50	IBA dip, IBA-50, none	3	20-42
	Dextrin—basal soaks or vacuum	16	6-62			
1952	Combinations of sucrose or dextrin, urea or alanine, IBA-50[3]	28	6-38	IBA-50, water, none, IBA-50	4	7-17
1953	2% sucrose + IBA-50 + a nitrogen source[4]	57	1-21	IBA-50, IBA dip; none	3	9-10
1954	1, 2, or 4% sucrose + .005, .01, .02, or .04M urea or alanine + IBA-50	48	1-17	Floramon; IBA dip; none; IBA-75	5	1-20
	Maleic hydrazide spray on trees at .025, .05, .10, and .20%	8	0-17			
1955	2% sucrose	2	5-10	IBA dip, 0.3% IBA, Floramon, IBA-50	4	7-35
	1, 2, or 4% sucrose + boron or urea or both[5]	16	3-32			

[1]Basal soaks in 5 percent solutions for 24 hours followed by a concentrated IBA dip.

[2]Levulose or dextrin solutions of 1, 2, and 4 percent; basal soaks or immersion in solution under partial vacuums up to 650 mm. of mercury for varying periods of time plus a concentrated IBA dip.

[3]Sucrose or dextrin solutions of 1 and 2 percent plus urea or alanine at 0.005, 0.02, 0.08, 0.32, and 1.28 molar plus IBA-50; also sucrose or dextrin at 0.5, 1, 2, and 4 percent with IBA-50.

[4]Nitrogen sources used at 0.005, 0.02, and 0.05 molar; sodium nitrate, ammonium nitrate, ammonium succinate, ammonium chloride, ammonium sulfate, ammonium tartrate, glutamic acid, glycine, tryptophane, aspartic acid, alanine, tyrosine, cystine, arginine, urea, peptone, and yeast extract. In general, 0.02 molar was the most favorable concentration.

[5]Boron at 5, 10, and 20 p.p.m.; urea solutions at .02M; all treatments included either IBA-50 or were followed by a dip into 0.3 percent IBA in talc.

Along with a few further trials in 1954 with cuttings soaked in urea or ammonium sulfate, trees were treated with maleic hydrazide in an effort to have stored starch converted to sugar (Greulach, 1953). Four groups of 5 trees each were sprayed with 3 gallons of maleic hydrazide solution at 1 of 4 concentrations: 0.025, 0.05, 0.10, and 0.20 percent. Cuttings were taken from the trees 2 weeks after spraying, and either soaked in an IBA solution or dipped in a talc dust of growth regulator. All treatments, however, were in the same range as that of the controls.

Reports that boron increased the translocation of sugar through cell membranes (Gauch and Duggar, 1953; Mitchell, Duggar, and Gauch, 1953) stimulated some trials with sugar, boron, and urea together with IBA in 1955. Rooting percentages, however, were in the same range as those obtained by treatments with growth regulators only.

Time required for rooting. Roots developed in the spring and summer of the year following placement of cuttings in the rooting beds. When cuttings were removed from the sand at the end of July, they ranged from the one extreme of having three or more roots up to several inches long (some even with small fibrous roots branching off) to the other extreme of no callus or root development at all, though the cutting was still alive. Many had only a ball of callus at the base. To determine whether cuttings with callus would have formed roots had they been allowed to remain longer in the rooting beds, callused cuttings were replaced after an initial examination the end of July. Most of these cuttings were given an additional IBA-50 soak, although some were not retreated. One lot of replaced cuttings was removed after an additional seven weeks in the beds; another was allowed to remain for one more year until July, 1952. A large majority (43) of the 66 groups of replaced cuttings, kept separate according to original treatment, contained over 20 cuttings per group, while the remaining groups contained from 4 to 20 cuttings.

The condition of the replaced cuttings deteriorated as the season progressed. At the end of the additional 7 weeks, most of the needles had turned brown, and some of the cuttings were dead, although the stems and buds of most of the cuttings were still alive and green. Practically all cuttings left in the bed for the additional year were dead at the end of this period.

Additional rooting, however, did occur on many of these replaced cuttings. There was an increase of 1 to 5 percent in the rooting percentages of 19 groups of cuttings, an increase of 6 to 10 percent in 9 groups, of 14 percent for 2 groups, of 18 percent for 1, and an increase of 28 percent in 1 other group. The great majority of increases in rooting percentage were with those groups (treatments) which had shown a relatively high rooting percentage at the time of first examination before being replaced in the cutting bed.

Another approach toward extending the rooting season, as well as eliminating losses during the winter period, was a trial in which winter cuttings (January, 1955) were flown to Lake City, Florida, and set out in outdoor rooting beds similar to the ones used in Wisconsin.[1] Rooting results from trials with simple growth regulator treatments were generally better than those from equivalent trials on summer cuttings (August, 1954) in Wisconsin. Thus, rooting of cuttings from 4-year-old trees ranged from 91 to 100 percent in Florida, from 57 to 95 percent in Wisconsin. Cuttings from 10-year-old seedlings showed from 34 to 43 percent rooting in Florida, 3-23 percent in Wisconsin; cuttings from 10-year-old trees which originated as rooted

[1]Grateful appreciation is due the U. S. Forest Service for assistance by the staff and use of the facilities of the Lake City Center, Southeastern Forest Experiment Station. Special thanks are due Pieter Hoekstra, Kenneth B. Pomeroy, and C. S. Schopmeyer.

cuttings, 35 to 50 percent in Florida, 2 to 18 per cent in Wisconsin. Unfortunately, the comparison had to be between cuttings taken in August, 1954, and overwintered in the usual manner in Wisconsin and cuttings taken in January, 1955, and placed immediately in the Florida cutting beds. Thus, the time at which cuttings were taken was a complicating factor.

Bottom heat. The effect of bottom heat in the rooting beds varied with the general conditions for rooting. Representative data are shown for 3 different years in Table 3. The difference in general rooting levels for these years can be seen by comparing rooting percentages in the controls for these years in Table 1. In a "good rooting year" (1951) bottom heat tended to increase both the percentage of rooting and the proportion of cuttings with more than 1 root. When conditions were somewhat less favorable, as in 1952, the effect of bottom heat was much less. In a year when rooting was very poor, as in 1956, bottom heat made it worse. The detrimental effect also appeared in good years with injurious treatments. Thus, with various high-nitrogen soaks, the amount of mortality was higher, and it occurred sooner in the heated bed than in the unheated beds.

Rooting of cuttings taken from previously rooted cuttings. For 7 years, cuttings were made from trees which had developed from rooted cuttings, and for comparison, from trees of seedling origin, both of which were established in a plantation near Wisconsin Rapids in 1945 (Patton and Riker, 1954). In addition numerous young rooted cuttings in Griffith Nursery from to 2 to 4 years old were available during the course of this work. Treatments varied somewhat from year to year, but always included the equivalent of a soak in indole-butyric acid at 50 p.p.m. for 24 hours. Other treatments sometimes included a concentrated IBA dip, a soak in water, or a dip into a plant regulator in dust form. All cuttings from the different sources each year were given identical treatments.

The summary of results (Table 4) shows that cuttings from trees which originated as rooted cuttings were consistently superior in rooting ability to cuttings from trees which originated as seedlings, until the trees were 9 years old. However, as the trees grew older there was a steady decline in rooting ability of cuttings from both types of trees, and from age 9 on the difference between the 2 sources had equalized. Cuttings from young rooted cuttings (Y.R.C.) were included most years as an additional check on rooting conditions. These continued to give a comparatively high rooting percentage when conditions were favorable for rooting.

Clonal variation. Variations in rooting ability among individual white pine trees

TABLE 3. Effect of bottom heat on percentage of rooting and on number of roots per cutting.

Year	Type of Bed	Total cuttings		Rooted cuttings with—		
		Treated	Rooted	1 root	2 roots	3+ roots
		No.	*Percent*	*Percent*	*Percent*	*Percent*
1951	Heated	1830	39	73	22	5
	Unheated	1830	30	84	14	2
1952	Heated	2010	14	78	18	4
	Unheated	2010	11	80	14	6
1956	Heated	1280	4	58	38	4
	Unheated	1280	6	51	27	22

TABLE 4. Rooting of cuttings taken from seedling trees and from trees grown from previously rooted cuttings.

Year of rooting	Age of plantation of cuttings and seedlings	Cutting source	Total cuttings	Cuttings rooted	
	Years		*No.*	*No.*	*Percent*
1950	6	Y.R.C.[1]	90	29	32
		R.C.[2]	90	36	40
		Seedlings[3]	90	21	23
1951	7	Y.R.C.	180	93	52
		R.C.	180	111	62
		Seedlings	180	102	57
1952	8	Y.R.C.	269	48	18
		R.C.	270	50	19
		Seedlings	270	20	7
1953	9	Y.R.C.	180	68	38
		R.C.	180	47	26
		Seedlings	180	49	27
1954	10	Y.R.C.	180	84	47
		R.C.	180	26	14
		Seedlings	180	23	13
1955	11	Y.R.C.	240	114	48
		R.C.	240	21	9
		Seedlings	240	24	10
1956	12	R.C.	180	4	2
		Seedlings	180	6	3

[1]Y.R.C. = Young rooted cuttings 2 to 4 years old in Griffith Nursery.
[2]R.C. = Trees in a plantation which originated as rooted cuttings.
[3]Seedlings = Trees in a plantation developed from seed.

are significant in a program concerned with selection for disease resistance. To investigate further clonal variation in rooting ability, cuttings were taken over a period of years from 10 selected trees in the Blister Rust Nursery—4 grafts and 6 seedlings. The grafts, which had been made with scions from mature trees, were 12 years old; the seedlings were 11 and 12 years old from seed. During the first 2 years 90 cuttings were taken from each tree, and during the next 3 years 60 cuttings. Cuttings were treated with an IBA-50 soak for 24 hours.

Differences in rooting percentages among the 10 clones for the years 1952 through 1955 are summarized in Figure 1. Environmental conditions for the fifth year (1955-56) were so adverse that all cuttings died and no measure of rooting ability was possible.

The average rooting percentages of the four graft clones 1 to 4, for the 4-year period, 1952-55, were 14, 7, 13, and 6, respectively, while those for the seedling clones 5 to 10 were 12, 19, 20, 23, 6, and 1, respectively. The data here and in Figure 1 indicate differences in rooting ability between clones. The over-all performance of clones 6, 7, and 8 was considerably above that of the others although large fluctuations occurred with these clones.

The rooting pattern showed marked fluctuation from year to year which was not uniform either in direction or in degree. Thus when some clones showed an

increase in rooting percentage during one year, others showed a decrease. In several cases, a suggestion appeared of alternate favorable years for certain clones.

The average rooting percentages of the 2-2 transplant controls for each of the 4 years were also plotted (on a different scale) in Figure 1. The effect of seasonal variation in rooting was reflected each year in the amount of rooting in these control cuttings. The marked fluctuations shown by many of the clones did not correspond to the seasonal fluctuation in rooting percentage exhibited by the control cuttings (Fig. 1).

Miscellaneous trials. Experience has shown that treatment of cuttings with growth regulators or with nutrient solutions was helpful only up to a certain point. Numerous other physical and chemical treatments were tried with no greater success, but because of their volume the data are omitted. Only some of the more extensive trials which might be of interest to other workers are listed here.

Treatments given cuttings included: hot water shock at temperatures of 35° to 50° C., basal wounds such as slits, shaved bark, tight wire girdles; basal wrappings with both semipermeable and impermeable materials; storage in moss and in sand at high and low temperatures, alone and in combination with wounding or with Vitamin B_1 treatments. Results were in the same range as the rooting percentages of cuttings from the same sources and given a standard IBA soak or dip treatment.

For one year's trials, cuttings were placed in the standard rooting medium (ordinary builder's sand) and also in three different mixtures of sand, peat compost, and commercial fertilizer. The watering cycle was reduced to 1 hour from a 15-minute cycle. Cuttings in sand only gave the best results, and increasing amounts of compost resulted in progressively poorer rooting, poorer callusing, and reduced general vigor.

A variety of treatments was applied to individual trees from which cuttings were taken subsequently: wire and steel-band girdles applied several years before cuttings were taken; cuttings notched at the base 1 week before removal from the tree;

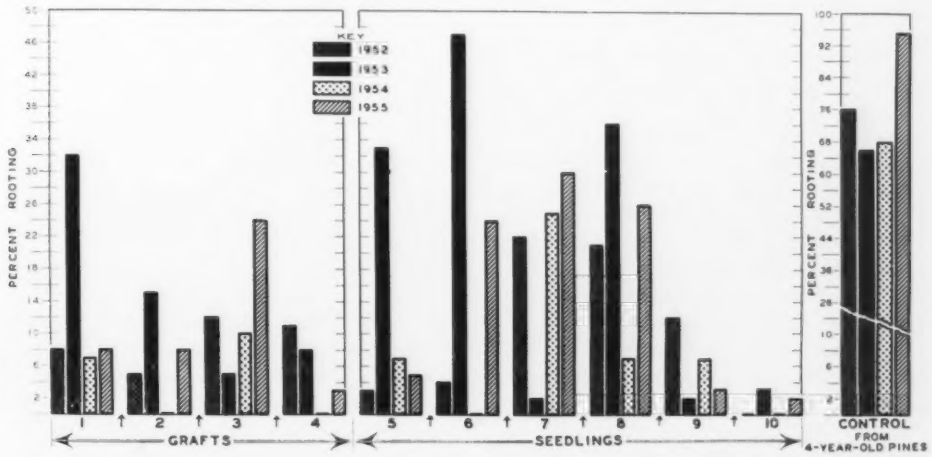

FIGURE 1. *Rooting of white pine cuttings originating during the 4-year period 1952-1955 from clones of 12-year-old grafts and seedlings. Rooting of control cuttings of 4-year-old nursery seedlings was plotted on a different scale.*

cuttings slit at the base and a lanolin paste of IBA applied to the cut 1 and 2 weeks before removal; trees sprayed with a solution of 2,4-D at 100 p.p.m.; trees sprayed with a solution of NAA at 100 p.p.m.; injection of plant growth regulators into the trunks, including either 2 percent sucrose plus 200 p.p.m. IBA, 500 p.p.m. naphthalene-acetamide, or 2 percent dextrin plus 200 p.p.m. IBA. Again rooting of cuttings from the trees before treatment or from similar trees in some cases, approximated rooting of those from the treated trees.

Two small trials of air layering were made: one of 143 air layers on 13 trees about 60 years of age, and one of about 25 on vigorous 15-year-old grafts from 40-60-year-old trees. The technique was similar to that described by Mergen (1955b). In the first trial established in July, 1954, only 35 were still green one year later, and only one had produced a root 1/16 in. long, which later died. All air layers in the second trial died before the end of the first summer.

Discussion

Root formation on cuttings involves the differentiation of a meristem into root primordia. Such differentiation is controlled by the balance between auxins and other plant constituents and is the physiological basis for rooting of cuttings (Leopold, 1955). The situation is extremely complex, however, and there are many individual factors which influence success of rooting. All must be in suitable balance for rooting. However, sometimes marked success is obtained when critical factors are not controlled or even known.

The extreme variation encountered from year to year was one of the most conspicuous results of the attempts at rooting of white pine cuttings over a period of several years. Certainly caution is advised in the interpretation of rooting results from only one year's experiments. Both "good" and "bad" rooting years were evident, resulting from inherent and environmental influences both while cuttings were still on the tree and after they had been placed in rooting beds.

Among the factors associated with successful rooting are those acting before the cuttings are made. The time of year when cuttings are taken has considerable effect upon the rooting percentages obtained. Cuttings taken in the fall or winter root much better in the greenhouse than those taken in the spring (Thomas and Riker, 1950; Doran, 1946). Fall cuttings in outdoor beds, however, suffered losses and interruption of the rooting process over the winter period, and also during the following summer. A recent approach with considerable promise is to make the cuttings from January to early March, place them in polyethylene bags, and store under refrigeration at below-freezing temperatures. As early as the cutting beds can be opened in the spring, cuttings are thawed slowly, a fresh cut made at the base, and the desired treatments applied. The cuttings are then inserted in the outdoor rooting beds to be left as long as necessary during the summer. Mulching of cuttings overwinter is thus eliminated.

The rooting ability of the individual tree from which cuttings are taken is another factor influencing success even before the cuttings are made. Clonal variation in rooting ability has been reported previously for white pine and other species (Doran, 1946; Deuber, 1942), and evidence for this also appeared in the present work. The extreme up and down fluctuations in alternate years were almost enough to suggest that there might be some cyclic variation in rooting response. Were such the case, this might help to explain some of the differences obtained in rooting response in different years and in the same year with separate lots of cuttings given identical treatments. Duffield and Liddicoet (1949) showed differences in rooting ability of individual seedlings and also found variation between the results of 2 successive years.

Age is one of the most important factors affecting rooting response. Although Thomas and Riker (1950) found no

clonal variation in rooting ability, it should be noted that all such trials were made with cuttings from grafts of older selections. The grafts maintained the "old-tree physiology" of the older trees from which the scions were taken, and the rooting response was so low in cuttings from all such trees that any original inherent differences in rooting ability probably were masked by the more dominant inhibitory influence of age upon rooting ability. Some suggestion to this effect may be found in the smaller differences that were noted in the present work among the 4 grafts than among the 6 seedlings. The problem of rooting cuttings from white pine trees which are "physiologically old" is one which may require the application of more subtle techniques than the type of empirical trials here reported. The nature of the changes which occur in the aging of the stock evidently lie at the heart of the matter.

Further evidence of the influence of age on rooting was provided by the response of cuttings taken from trees which originated as rooted cuttings. The better rooting ability for the first few years of cuttings from trees grown from previously rooted cuttings over that of cuttings from trees of seedling origin held promise as a means of developing clones that would root easily by a process of continual rooting from young stock. However, as the trees developed from rooted cuttings grew older, there was a steady decline in rooting ability of cuttings from them. An interesting series of trials with white pine cuttings over a period of 16 years by De Lisle (1954) showed even more clearly the influence of age. Rooted cuttings planted in 1938 were allowed to grow to 4-year saplings, and then cuttings from these were rooted and planted. The process was repeated every 4 years through 1954. Rooting ability decreased markedly with each subsequent replication. The physiological age of the stock continued to increase, and some of the saplings produced cones in 1953-54, indicating a transition to the reproductive stage.

Various factors are important also after the cuttings are removed from the tree. Adjustments in minor maintenance procedures, such as spray interval, spacing, and fertilization, did not markedly influence the vigor of cuttings in the rooting beds. However, the rooting medium and temperature were influential in affecting rooting and condition of the cuttings. Bottom heat seemed to serve largely in a supplementary capacity, emphasizing the influence of favorable or unfavorable factors, which included various types of chemical treatments.

Carbohydrates and nitrogenous substances are especially important in the interaction between auxins and other plant constituents in the root-forming process. From the correlation by many workers of the ease of rooting with carbohydrate reserves has come a generalization that for optimum rooting the ratio of C to N should be high (Leopold, 1955). Some evidence along this line appeared in the present work, but in all the trials with carbohydrate and nitrogen sources applied by basal soaks, partial vacuum treatments, or tree injection, the results were extremely inconsistent. From time to time there were indications that treatment with sugar and urea had some value, but just as often results from another year or another series of treatments failed to substantiate their worth. The literature is full of conflicting reports as to the efficacy of such treatments, possibly because of failure to understand or control the interaction with auxins.

The plant growth regulators, it would appear, still hold the key to root formation on cuttings. With a clearer definition of the exact nature of their role in the complex interaction between them and the other organic materials in plants may come more effective methods of stimulating root formation on cuttings.

Summary

During the period between 1949 and 1956, investigations on the rooting of eastern white pine cuttings were continued in outdoor propagating beds under an automatic

sprinkler system. "Control cuttings" from 2-2 nursery transplants generally rooted from 30 to over 90 percent after treatment with indole-butyric acid. Variations from year to year in the general level of rooting of these controls served as an "index" of rooting conditions, against which rooting of cuttings from older trees could be compared.

The use of plant growth regulators, primarily indole-butyric acid, was necessary as a standard procedure upon which other supplementary treatments were based.

Common builder's sand as a rooting medium was preferable to a sand-peat compost mixture. Bottom heat supplied by electric heating cables tended to increase rooting in "good rooting years," but had a detrimental effect when rooting treatments were somewhat injurious to the cuttings, or in years when the general rooting level was low.

No single treatment in which various sugars or nitrogen sources were applied was found that consistently promoted a relatively high percentage of rooting from older-tree cuttings.

Variable results also ensued from numerous miscellaneous trials. Air layering on 60-year-old trees and on 15-year-old grafts from 60-year-old trees was not successful.

Distinct differences in rooting ability among several clones appeared over a 4-year period. Several of the clones exhibited extreme fluctuations in rooting ability from year to year which did not correspond with the seasonal fluctuations in rooting as reflected in the controls from 2-2 stock.

Rooting of cuttings from trees which originated as rooted cuttings was superior to that of cuttings from trees of seedling origin until the trees were 9 years old. As the trees grew older the rooting ability of cuttings from both types of trees declined, and from age 9 on the difference between the 2 sources had equalized.

One of the major disadvantages in handling cuttings made near the end of the summer was the necessity for carrying the cuttings in outdoor propagating beds through the winter. Recent limited trials indicated that a more advantageous procedure would be to take cuttings in late winter, store them under refrigeration until early spring, and leave them in the cutting beds for as long as necessary in the summer to get maximum rooting.

Literature Cited

DELISLE, A. L. 1954. The relationship between the age of the tree and the rooting of cuttings in white pine. (Abstr.) Proc. Indiana Acad. Sci. 64: 60-61.

DEUBER, C. G. 1942. The vegetative propagation of eastern white pine and other 5-needled pines. J. Arnold Arboretum (Harvard Univ.) 23: 198-215.

DORAN, W. L. 1946. Vegetative propagation of white pine. Mass. Agric. Expt. Sta. Bull. 435, 16 pp.

DUFFIELD, J. W., and A. R. LIDDICOET. 1949. Variability of rooting in a small second generation population of the hybrid *Pinus attenuradiata*. J. For. 47: 107-109.

GAUCH, H. G., and W. M. DUGGAR, JR. 1953. The role of boron in the translocation of sucrose. Plant Physiol. 28: 457-466.

GRUELACH, V. A. 1953. Notes on the starch metabolism of plants treated with maleic hydrazide. Botan. Gaz. 114: 480-481.

HEIMBURGER, C. 1956. Blister rust resistance in white pine. *In*, Proc. 3rd Northeastern Forest Tree Improvement Conf., Aug. 30-31, 1955. pp. 6-13.

LEOPOLD, A. C. 1955. Auxins and plant growth. Univ. of California Press, Berkeley and Los Angeles. 354 pp.

MERGEN, FRANCOIS. 1955a. Vegetative propagation of slash pine. Southeast. For. Expt. Sta., Paper No. 54, 63 pp.

———. 1955b. Air-layering of slash pines. J. For. 53: 265-270.

MITCHELL, J. W., W. M. DUGGAR, JR., and H. G. GAUCH. 1953. Increased

translocation of plant-growth-modifying substances due to application of boron. Science 118: 354-355.

PATTON, R. F., and A. J. RIKER. 1954. Top growth and root development of rooted white pine cuttings. J. For. 52: 675-677.

THOMAS, J. E., and A. J. RIKER. 1950. Progress on rooting cuttings of white pine. J. For. 48: 474-480.

Quantitative Plant Ecology

By Greig-Smith, P. 1957. Academic Press Inc., New York, and Butterworths Scientific Publications, London. 198 pp. $6.00.

Review by A. L. McComb,
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Plant ecology is undergoing transition from a qualitative to a more quantitative science. The transition is difficult because the science is complex and suffers from a large number of interacting variables, many of which cannot be adequately controlled and subjected to precise measurement.

The author of this book, who is lecturer in botany at the University of North Wales, has attempted to make the transition easier by describing the quantitative methods of ecology and the application of statistical methods to ecological problems. His assessment of the practical potentialities of these methods is well worth attention. He brings to his task a good grasp of the principles, problems and methodology of ecology and of statistical methods.

Chapter I discusses the methods of quantitatively describing vegetation, including frequency, density, percentage of cover, basal area area and yield. Methods of sampling, particularly number and position of samples and comparison of results of different sets of observations are treated in Chapter II.

Pattern, i.e., the departure from randomness of the individuals within the community, occupies Chapter III. Departure from randomness is important primarily becaues it is a guide to the factor or factors affecting the survival of individuals and controlling community composition. The techniques for detection and analysis of non-random distribution are extensively treated. A conclusion emerging is that individuals within a species are rarely randomly distributed.

Chapter IV deals with association between species in the community. "If several species in a community exhibit pattern, indicating control by influencing factors, study of association between them will provide evidence of any groupings of the species into assemblages of like response to the influencing factor or factors."

Correlation of vegetation with habitat factors is the subject of Chapter V. Four combinations of qualitative and quantitative data are considered.

The delineation of plant communities based on floristic composition, species abundance, performance of species, growth and life form, physiognomy, pattern of constituent species and various mathematical constants derived from other criteria is discussed in Chapter VI. This leads to a consideration of the classification of vegetation, whether a natural classification is possible and if so, how it may be achieved. Here enters a little of the current controversy in Ecology, especially the notion of a community as an organism and whether vegetational communities are discrete entities or merely parts of a continuum.

The final chapter gives the author's views on the contribution of the quantitative approach to ecological theory. It is followed by two brief appendices.

Reading this book with understanding presupposes a good working knowledge of statistical and ecological methodology and it will not be easy for the beginner in either field. More topic headings would have made reading easier. Much data from recent ecological literature is introduced, statistical procedures illustrated and problems discussed. The author is well aware of both the limitations and advantages of statistical treatment of ecological data and judgments, when made, seem balnced and sound. This book should prove valuable to research workers and graduate students in forestry, range management, botany and allied disciplines.

Hydrogen Peroxide for Rapid Viability Tests of Some Coniferous Tree Seeds

BY
TE MAY CHING
M. C. PARKER

THE VIABILITY of a seed lot is usually indicated by its germination potential as determined by an accepted laboratory germination procedure. Most tree seeds require a long period of stratification in order to obtain a prompt and uniform germination. Thus a rapid and reliable viability test is needed to facilitate the seed testing in business transactions as well as nursery practice or direct seeding.

Reported here is a method that has proven successful on seeds of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine (*Pinus ponderosa* Laws), sugar pine (*P. lambertiana* Dougl.), jeffrey pine (*P. jeffreyi* Grev. & Balf.), lodgepole (shore) pine (*P. contorta* Dougl.), noble fir (*Abies procera* Rehd.), grand fir (*A. grandis* (Dougl.) Lindl.) and white fir (*A. concolor* (Gord. & Glend.) Lindl.).

Previous Work

A large number of rapid viability tests have been proposed. These range from simple visual observations of seed appearance to complex biochemical analyses. Baldwin (1942) lists and describes physical and biochemical methods of determining seed viability without germination and presents an extensive bibliography on the subject. Many of the techniques reviewed by Baldwin require special apparatus and precise control of detailed procedures. The simpler techniques, such as the cutting test, are subject to obvious limitations.

More recently the use of tetrazolium salts[1] for vital staining of seed in order to evaluate viability has found considerable acceptance, especially with European workers (Lakon, 1950). Flemion and Poole (1948) and others have cautioned against placing complete reliance on the tetrazolium staining reaction as a criterion of seed viability.

The excised embryo technique perfected by Flemion (1948) is a more reliable method since it is a direct viability test. Considerable skill is required, however, on the part of the technician and the process is slow and tedious.

[1]Editor's note: See also article by Charles X. Grano. Tetrazolium Chloride to Test Loblolly Pine Seed Viability. For. Science: 4:42. 1958.

The authors are Assistant Agronomist and former Assistant Agronomist respectively, Cooperative Seed Laboratory, Oregon Agricultural Experiment Station. The project was conducted cooperatively by the Oregon Seed Laboratory of the Agricultural Experiment Station, the Oregon Forest Protection and Conservation Committee and the Forest Tree Seed Committee affiliated with the Western Forestry and Conservation Association. Technical Paper Number 1074. Oregon Agricultural Experiment Station.

The earliest references to the use of hydrogen peroxide on seed are by Miége (1908) and by Babcock (1911). Miége used hydrogen peroxide as a fungicide for treating wheat seed infected by smut and found that this reagent was poisonous when used in strong solutions. Dilute solutions facilitated germination and stimulated the seedlings to more active development. Babcock used H_2O_2 as a seed sterilant in germination studies and noticed a stimulating effect on the seeds of barley, wheat, rye, corn, buckwheat, peas and beans. Babcock also recognized that the oxygen needed for respiration by the submerged seed was obtained from the reagent.

Gilbert *et al.* (1954) used hydrogen peroxide solutions for production of seminal roots (chitting) of malting barley seed. Parker and Hill (1955) suggested the use of dilute solutions of hydrogen peroxide for rapid evaluation of malting barley viability as an additional factor to be considered in barley grading when time for a standard laboratory germination test was not available.

No references were found on the use of hydrogen peroxide for testing viability of tree seeds. However, it has been used in a standard catalase activity determination with finely ground pine seed. Catalase is an enzyme capable of decomposing hydrogen peroxide to liberate oxygen. Fairly close correlations have been found between catalase activity and germination (Leggatt, 1929). Reliable determinations of catalase activity require special apparatus and careful attention to test conditions. The catalase activity test is not in general use for evaluating viability of coniferous tree seeds.

The method reported here makes use of hydrogen peroxide solutions combined with simple techniques to obtain reproducible direct viability readings in a short time.

Materials and Methods

The majority of the seed lots used in this study were collected especially for experimental purposes by members of the Northwestern Forest Tree Seed Committee over a three-year period from 1954-56 from varying altitudes in Oregon and Washington. Samples of tree seeds received by the Laboratory for routine service tests were also utilized. All lots were cleaned to highest cutting test possible by a South Dakota Blower with proper maximum blowing points. Cleaned seeds were stored in a cool room at 0-3° C. until used.

The test procedure consists of soaking the seed in hydrogen peroxide solutions after opening the seed to permit rapid absorption of the solution.

Duplicates of 50 seeds were used to evaluate each lot. The radicle end (Example: the darker colored tip on ventral side of Douglas-fir seed) of each seed is opened either by cutting with a razor blade or by sanding. A very satisfactory method of opening seed of the larger seeded pine species consists of sanding them on a motor-driven sander such as a face plate carrying 100 to 220 grit sanding paper. It is necessary to cut through the outer seed coat and inner seed coat membranes which will result in cutting into the endosperm and removal of the tip of the embryo radicle. While depth of cut is not critical, "shallow" sanding or cutting is preferable to "deep" cutting since removal of an excessive portion of the embryo should be avoided.

The opened seed is placed in a 1.0% aqueous solution of hydrogen peroxide making certain that each seed is wetted. Volume of solution varies with the size of the seed; the volumes listed in Table 1 for each kind of seed are the optimums so far tested. Glass beakers or plastic refrigerator dishes of 350 ml. capacity are satisfactory containers. They should be loosely covered to reduce evaporation. For most species of conifers the containers of solution with seed being tested are kept at 20° C. Douglas-fir and noble fir are tested at an alternating temperature of 20°-30° C. (16 hours at 20° C. and 8 hours at 30° C.). The testing temperature is rather non-specific. The temperatures used here are the satisfactory

TABLE 1. Methods used for hydrogen peroxide test and germination test of the various species of coniferous tree seeds.

Species	Hydrogen peroxide test[1]			Germination test			
	Volume/ 50 seed	Testing temp.	Test duration	Water soaking	Moist strat.	Germ. temp.	Test duration
	ml.	*Degrees C.*	*Days*	*Hours*	*Weeks*	*Degrees C.*	*Days*
Pinus contorta	120	20	5	none	4	15-30	42
Pinus jeffreyi	150	20	5	16	8	20-30	49-70
Pinus lambertiana	300	20	6	none	8	15-30	90
Pinus ponderosa	300	20	7	24	4	20 or 20-30	56-77
Abies procera	150	20-30	9	36	4	20-30	49-70
Abies grandis	150	20-30	8	36	4	20-30	49-70
Abies concolor	150	20-30	9	36	4	20-30	49-70
Pseudotsuga menziesii	150	20-30	5	none	2	20-30	35-49

[1]The strength of solution was 1% in each case.

ones tested so far. The seed is kept in the solution for the duration of the test. Douglas-fir can be tested in 5 days and ponderosa pine in 7 days. A schedule of the testing methods employed is presented in Table 1 and the comparative results in Table 2. Seeds with elongated radicle (1-8 mm.) are classified as viable and the ones without visible growth at the end of the test period are classed as non-viable (Figs. 1 and 3). The viable percentage is calculated from the average of the two replicates provided the difference between them is less than 10, otherwise the seed lot is retested.

The validity of this hydrogen peroxide test in Douglas-fir seed was checked by the germination percentages obtained from the same seed lot, as well as by conducting a subsequent growth test on the actual seeds which had been classified as viable by the hydrogen peroxide test. This subsequent growth test was done by removing the viable seeds (with elongated radicle) from the test solution daily, transplanting them to sterilized moist sand in petri dishes, then incubating them in a germination cabinet at 20°-30° C.

The germination method used for the percentages reported in Table 3 is the accepted procedure used in the Oregon Seed Laboratory for testing Douglas-fir. The procedure is to space duplicates of 100 seeds on moist sand in a non-toxic plastic sandwich box, chill at 5° C. for two weeks then germinate at 20°-30° C. The test is supplemented with eight hours of fluorescent light daily for 3-5 weeks. The germinated seedlings are counted at weekly intervals. The cumulative numbers of germinated seedlings is considered the total germination percentage. If the difference between replicates is larger than 10 the seed lot is retested.

Results and Discussion

Any quick viability test of seeds should have the virtue of reproducibility and must also have a close correlation with an accepted germination test. Table 4 lists the results of replicated hydrogen peroxide tests performed by different personnel at different times and under various conditions. These four sets of results when subjected to a complete analysis of variance were found to exhibit no significant differences between them; in other words the test is reproducible under these conditions.

Tables 2 and 3 summarize the results of hydrogen peroxide tests and corresponding germination tests. The correlation coefficient (r) in both tables indicates a significant correlation between the two tests. Further analysis of the differences between the paired observations showed that in Table 2, the average viability determined by hydrogen peroxide method is 3.364 ± 1.237 percent higher than that of germination test, while the average difference in Douglas-fir is 3.320 ± 0.901 percent (Table 3). These differences could be attributed to the sound seeds remaining after the germination test, for the range of sound seeds found at the end of the test was 0 to 8 percent in the samples studied.

The validity measurement using subsequent growth from seeds classified as viable in the peroxide test is the more direct ap-

TABLE 2. Viability percentages obtained from the hydrogen peroxide test and from accepted laboratory germination testing methods.[1]

Species	Lot No.	Hydrogen peroxide test	Germination test
Pinus contorta	31580R	96	94
Pinus jeffreyi	33297R	96	94
	34819R	84	85
	34820R	76	76
Pinus lambertiana	.....	84	78
Pinus ponderosa	Wenatchee	99	94
	DL55	89	86
	PP54-1	92	80
	PP54-2	24	29
	PP54-3	80	83
	PP54-4	73	71
	PP54-5	82	81
	PP54-6	78	81
	PP54-7	71	68
Abies procera	NF54-1	69	68
	NF54-7	67	57
	NF54-10	36	34
Abies grandis	64614R	60	50
	64615R	83	64
	64616R	27	24
Abies concolor	64618R	39	41
	64619R	75	64

[1]Correlation coefficient (r) = .995 (significantly correlated). Hydrogen peroxide test = germination test + 3.364 ± 1.237.

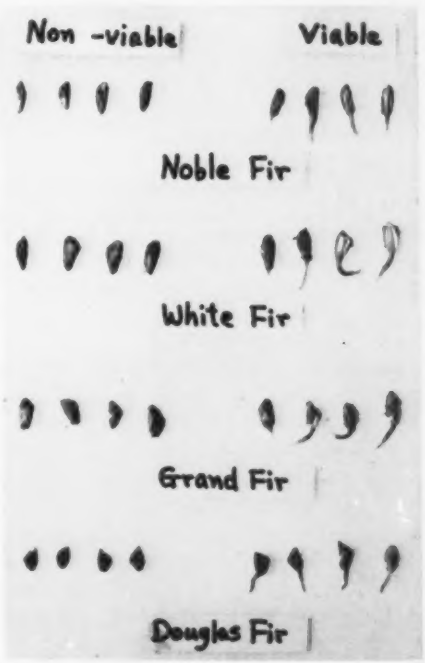

FIGURE 1. *Typical viable and non-viable seeds of various species as classified following the hydrogen peroxide test.*

proach. However, the depth of cut into embryo tissue and the amount of hydrogen peroxide solution absorbed are beyond experimental control. The invasion by microorganisms and interaction of hydrogen peroxide with enzymes and/or metabolites in the tissues plays a very important role in the subsequent growth test. Only a limited number of such experiments were carried out. Survival rates of viable seeds were 50 to 84 percent for Douglas-fir, 18 to 40 percent for ponderosa pine and 20 to 47 percent for true firs. The seedlings were somewhat stubby and short-rooted due to a lack of root meristematic tissue which was removed at the beginning of the test (Fig. 2).

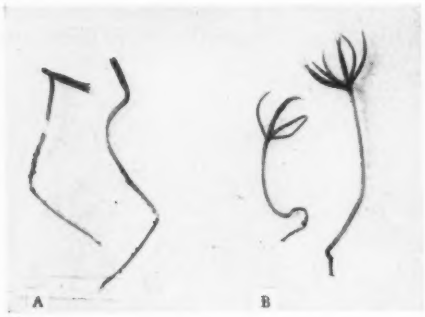

FIGURE 2. *Comparison of Douglas-fir seedlings obtained from* A, *laboratory germination test (one week old) and* B, *seedlings (3 weeks old) grown from seed classified as viable in hydrogen peroxide test.*

FIGURE 3. *Viable seed of ponderosa pine at conclusion of hydrogen peroxide test. Seeds on right sectioned to illustrate amount of embryo development.*

TABLE 3. Comparison of percentages of viable seeds of Douglas-fir determined by hydrogen peroxide test (5 days) with germination test (35-49 days).[1]

Seed Lot	Peroxide	Germination
	Percent	*Percent*
DF54-1	92.25	82.50
DF54-2	88.00	75.50
DF54-3	86.50	80.50
DF54-4	90.00	86.50
DF54-5	88.50	81.00
DF55-1	92.00	92.50
DF55-2	91.50	86.00
DF55-3	88.50	87.00
DF55-4	93.00	87.00
DF55-5	88.25	76.00
56944R	70.00	68.00
57423R	89.00	87.00
57510R	79.00	75.00
58150R	80.00	80.00
58151R	88.00	92.00
58152R	87.00	92.00
58153R	94.00	98.00
58154R	96.00	89.00
58155R	97.00	86.00
58156R	94.00	92.00
58157R	88.00	77.00
58158R	91.00	90.00
58352R	88.00	79.00
59223R	89.00	82.00
59224R	92.00	87.00
59225R	93.00	90.00
59226R	98.00	93.00
59227R	95.00	92.00
59228R	75.00	72.00
59229R	86.00	95.00
59230R	84.00	85.00
59231R	87.00	84.00
59237R	88.00	94.00
59238R	82.00	82.00

[1] $r = .694$ (significantly correlated). Hydrogen peroxide test = germination test + 3.320 ± 0.901.

TABLE 4. The percentages of viable seed of Douglas-fir lots determined by hydrogen peroxide tests performed under different conditions at different times.[1]

	Five-day test		Seven-day test		
	Controlled temperature dark		Room temperature daylight		
Seed lot	20°-30° C. Oct. 20, 1956	20°-30° C. Dec. 31, 1956	16°-25° C. Jan. 17, 1957	18°-26° C. Apr. 12, 1957	Average
DF54-1	89	94	91	95	92.25
DF54-2	90	93	79	90	88.00
DF54-3	92	84	86	84	86.50
DF54-4	96	90	86	88	90.00
DF54-5	92	88	82	92	88.50
DF55-1	92	95	91	90	92.00
DF55-2	84	95	89	98	91.50
DF55-3	86	90	88	90	88.50
DF55-4	91	94	95	92	93.00
DF55-5	89	89	94	81	88.25
DF56-1	83	72	84	78	79.25
DF56-2	72	70	69	81	73.00
DF56-3	90	91	88	96	91.25
DF56-4	93	92	90	96	92.75
DF56-5	97	98	91	99	96.25
Average	89.06	89.00	86.86	90.00	88.73

[1]L.S.D. at 5% level = 3.270. L.S.D. at 1% level = 4.537.

The hydrogen peroxide viability test has several distinct merits over other presently available rapid viability tests for tree seeds. It is a direct viability test since actual growth is produced; it is simple to perform and anyone following the technique with care should succeed in obtaining reliable results; and the method overcomes or bypasses seed dormancy. Tests with freshly harvested lots which require moist stratification prior to germination responded readily to the hydrogen peroxide treatment. None of the seed lots tested in this study failed to respond within 10 days in the solution.

The hydrogen peroxide method of determining viability of coniferous tree seed promises to become a usable test when limited time is available for an evaluation of the seed but is not intended to replace laboratory germination tests. Well conducted germination tests permit discovery of the presence of abnormal seedlings, the recognition of certain pathological conditions, and the use of chilling or stratification techniques prior to germination, all of which can contribute useful information of benefit to nurserymen and other seed users.

Summary

The viability or percentage of live seed of seed lots of some coniferous tree species may be determined in 5 to 9 days after the seed are steeped in 1 percent aqueous solutions of hydrogen peroxide following removal of the radicle end of the seed by cutting or sanding. Douglas-fir seed is tested at alternating temperatures of 20°-30° C. in 150 ml. of solution per 50 seeds, and ponderosa pine at a constant temperature of 20° C. in 300 ml. of solution per 50 seeds. Volume of solution and temperature requirements for other species are tabulated. Viable seeds produce visible radicle development within the test period.

Accuracy of the testing method was de-

termined for Douglas-fir seed by application of statistical analysis which indicated the method to be reproducible and to be significantly correlated with accepted laboratory germination tests.

Freshly harvested or dormant seed responds as readily as non-dormant seed.

Literature Cited

BABCOCK, S. M. 1911. Metabolic Water: Its production and role in vital phenomena. Wisc. State Res. Bull. 22, pp. 87-181.

BALDWIN, H. I. 1942. Forest Tree Seed of the North Temperate Regions. Chronica Botanica Co., Waltham, Mass. 240 pp.

FLEMION, F. 1948. Reliability of the excised embryo method as a rapid test for determining the germinative capacity of dormant seeds. Contrib. Boyce Thompson Inst. 15:229-241.

FLEMION, F., and H. POOLE. 1948. Seed viability tests with 2, 3, 5-Triphenyl tetrazolium chloride. Contrib. Boyce Thompson Inst. 15(4): 243-258.

GILBERT, S. G., P. H. BLUM and A. FRIEDEN. 1954. The inhibition of barley germination by steep liquor. Proc. Amer. Soc. Brewing Chemists, 1954, pp. 51-56.

LAKON, G. 1950. Die Feststellung der Keimfahigkeit der Koniferensamen nach dem Topographischen Tetrazolium-Verfahren. Saatgut-Wirtschaft 4, 2, pp. 83-87.

LEGGATT, C. W. 1929. Catalase activity as a measure of seed viability. Sci. Agric. 10:73-110.

MIE'GE, E. 1908. Traitement des Semences par l'eau Oxygenee. Ann. Ecole Nat. Agric. Rennes 11. (Abstracted in The Gardener's Chronicle, 1911, 50 (1292), page 241, Treatment of Seeds with Hydrogen Peroxide.)

PARKER, M. C., and D. D. HILL. 1955. Hydrogen peroxide solutions for rapid determination of barley viability. Agronomy Absts., 1955, pg. 71.

SNEDECOR, G. W. 1946. Statistical methods. 4th ed. Iowa State College Press.

Studies of Regeneration in Forest Stands Devastated by the Spruce Budworm

II. Age, Height Growth, and Related Studies of Balsam Fir Seedlings

BY
A. W. GHENT

DIFFERENCES OF OPINION on the role of the spruce budworm (*Choristoneura fumerana* Clem.) in forest succession have centered on two main issues: first, that budworm outbreaks might have a consistent influence upon the proportions of spruce (white spruce, *Picea glauca* (Moench) Voss and black spruce, *Picea mariana* (Mill.) B.S.P.) and of balsam fir (*Abies balsamea* (L.) Mill.) in subsequent stands; and second, that such an influence might come about through a difference in the ability of spruce and balsam fir seed trees to survive an outbreak and from differences in the rooting ability and competitive vigor of their seedlings. Part I of this series (Ghent *et al.*, 1957) treated the changes in the proportions of spruce and balsam fir in selected study areas during the first decade following budworm devastation. It was concluded in that paper that although the apparent trend in forest succession might be consistent within the region of one outbreak, an equally consistent but exactly opposite trend might be observed within the region of another, so that the problem could not be resolved at this level of generality. In the same paper, it was shown that height growth of spruce and balsam fir seedlings was strikingly similar both before and after the devastation of the overstory trees by the spruce budworm, and that no gross differences in competitive vigor seemed to exist.

In the suggestion that a budworm outbreak might influence succession through differences in the survival of seed trees or in the rooting ability of seedlings, it is clearly implied that the seedlings that grow to form the next stand originate either

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Gratitude is expressed by the author to many associates who have been of assistance during the field studies and the preparation of the manuscript, in particular R. M. Belyea and M. L. Prebble of the Forest Biology Division. W. E. Cawthray and H. D. Haswell, formerly of this laboratory, generously permitted some of their unpublished data to be incorporated in the calculations of seed productivity.

during or immediately after the period of budworm devastation. deGryse (1944) refers to the "extraordinary accumulation of debris on the surface" following a budworm outbreak as hampering the regeneration of spruce while seemingly offering no obstacle to balsam fir. Silvicultural practices designed to regenerate the forest from seed trees left after logging may have contributed to the idea that a post-budworm forest necessarily develops from post-budworm seed production; and in the same way the well established pruning and girdling techniques in orchard and nursery practice designed to elicit heavy fruit or seed production may have contributed to the notion of the "distress" seed crop. However this may be, inspection of even a few seedlings at the beginning of the present study sufficed to suggest that these patterns of thinking had been carried over somewhat uncritically in the earlier spruce budworm literature, and for this reason the determination of the history of establishment of seedlings was incorporated as a major facet of our regeneration research.

The main purpose of this paper is to present data on the history of establishment of balsam fir seedlings in the area of the Lake Nipigon-Black Sturgeon Lake outbreak of the 1940 decade. The Forest Insect Laboratory in Sault Ste. Marie maintains field stations in three areas of severe budworm damage: at Laniel in the Province of Quebec adjacent to the northeast boundary of Ontario, at Black Sturgeon Lake north of Lake Superior, and at Cedar Lake in northwestern Ontario. Of these the Black Sturgeon Lake area seemed best suited for an intensive study of seedling establishment. At Cedar Lake the budworm outbreak was still in progress at the time this study was started, so that any conclusions drawn solely from data gathered in this area would necessarily have been tentative. The budworm outbreak at Laniel was complete, but the history of defoliation of particular portions of the general outbreak area was only sketchily known. Less intensive investigations were conducted in both of these outbreak areas, however, by J. B. Thomas at Laniel, and by J. R. Rooke at Cedar Lake, and the results confirmed the picture of seedling establishment obtained from the Black Sturgeon Lake study.

Directly related to the problem of seedling establishment is the question of seedling height growth. Balsam fir seedlings are well known for their tolerance of intense shade and presumably intense root competition, though this tolerance is expressed by their tenacious survival rather than by their growth rate under these conditions. Many of the balsam fir seedlings in budworm-devastated areas appeared on casual inspection to be vigorous, fast-growing seedlings of recent origin, though closer inspection revealed that these had earlier endured many years of severely suppressed growth. This study afforded the opportunity to establish that recent vigorous growth was in fact an expression of the release of the seedlings rather than a coincidence of a few unusually favorable growth years, and in addition the opportunity to determine the approximate point in the sequence of progressive defoliation and mortality at which such release began to be expressed.

A by-product of the study of height growth was a brief investigation of the production of terminal-lateral buds — those buds that give rise to the whorl of branches at each successive node. The production of these buds appears to be closely related to the increment in height growth of the current year, and data on this relationship are included in the present paper. Also arising from the close scrutiny accorded the height growth of seedlings is a technique for obtaining the history of a recently completed budworm outbreak from the evidence of damage to seedlings caused by the feeding of late-instar larvae, and an account of this technique is also included. Finally, data from several other investigations in the Black Sturgeon Lake area have been brought together in an attempt to as-

sess the numerical relations of seed production and seedling establishment under forest conditions.

Age of Balsam Fir Seedlings in Relation to the Budworm Outbreak

Regeneration studies at Black Sturgeon Lake reported here have been conducted on 11 permanent study plots, selected to give a representative cross-section of forest and site conditions in the area that was devastated by the spruce budworm. The determinations were restricted to balsam fir seedlings, since they were from 10 to 200 times more abundant than spruce seedlings and could be removed in adequate numbers from the peripheral areas of the plots without appreciable effect on the composition or abundance of the regeneration.

Age determinations were based on ring counts at ground level. Evidence from small seedlings pulled by the roots indicated that ground level might give a slightly conservative estimate of seedling age, for on some seedlings leaf scars were found below the uppermost roots. These were apparently adventitious roots that had developed as moss and humus accumulated about the base of the seedlings. Despite this, ground level was used as the one point that could be determined conveniently and uniformly for all seedlings. Ring counts were made on smoothly-cut basal sections of the seedlings with the aid of a binocular dissecting microscope, and preliminary tests indicated a high reliability for the technique employed.

Since an accurate tally of the distribution of seedlings by height classes was already available for each study plot, it was expedient to sample for age distribution by height classification. These samples were restricted to 5 height classes between ground level and 42 inches, since these classes were known to include over 97 percent of the seedlings at that time. Separate collections of 35 to 40 seedlings were made for each height class on each plot. The 11 study plots yielded 42 separate collections, some plots having seedlings in only 3 or 4 of the 5 classes. Our knowledge of the history of establishment of balsam fir seedlings in this area is therefore based on ring-counts performed on more than 1500 individual seedlings.

Each of the 11 study plots has been given equal weight in the analysis on the assumption that, taken together, they would represent a proportionate sample of the various forest conditions susceptible to the budworm in the Black Sturgeon Lake area. Since a nearly identical picture was obtained for each plot, the presentation of this mass of data as one picture for the entire Black Sturgeon Lake area seems clearly justified.

These data are presented in Figure 1. The visual impression obtained from the figure of the relative importance of each of the 5 height classes may be accepted as

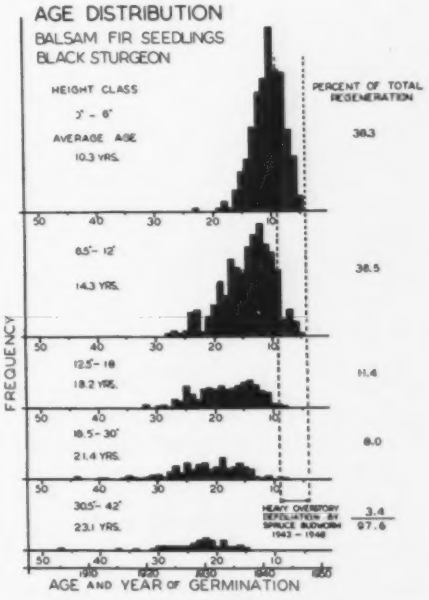

FIGURE 1. *Age Distributions by height classes for combined samples of balsam fir seedlings from 11 study plots in the Black Sturgeon Lake area. Histogram areas are in proportion to the percentage of each height class in the seedling population.*

realistic. In the preparation of this figure age distributions within each height class were accumulated from the 11 plots. The observed pattern of histogram bars were retained and at the same time the areas of the five histograms were adjusted so these areas would bear the same relation to each other as the numbers of seedlings occurring in the corresponding height classes had borne in the field. No ordinate scale is given in this figure: the highest of the individual histogram bars represents only slightly over 1 percent of the total population of seedlings, so that an ordinate scale would have been of no interpretative value.

The period of heaviest overstory defoliation from 1943 to 1948 is indicated in Figure 1 by vertical dotted lines. The selection of 1943 as the beginning of this period is somewhat arbitrary, since heavy defoliation occurred in the overstories of some of the more northerly plots in 1942. For 7 of the 11 plots, however, 1943 was the more realistic choice, and on this basis over 80 percent of the total area of these 5 histograms falls to the left of the first of these dotted lines. This percentage is calculated from the apparent year of germination of the seedlings, however, and gives only a part of the over-all picture. Seedlings that germinated in 1944, for example, originated as seed in cones that ripened in 1943, which in turn were initiated as flower buds on the shoot growth of 1942. If one thinks of the flower initiation that made possible the eventual establishment of the seedlings represented in Figure 1, the effect is to shift the relative position of the dotted lines representing the period of peak budworm populations 2 years to the right towards more recent times, or conversely and more accurately, to shift all the histograms 2 years to the left. On this basis alone it is possible to say that 93 percent of all balsam fir seedlings present in the Black Sturgeon Lake area in 1950 could be attributed to the flower production of 1942 or earlier. Considering in addition the earlier observation that ground-level age estimates of balsam fir seedlings are prone to conservative bias, it becomes apparent that the sequence of balsam fir flower production and seedling establishment came to its end, rather than its beginning, with the onset of heavy defoliation by the spruce budworm.

This conclusion from the data on seedling establishment was substantiated by direct observation of the remnant cone spikes of a few balsam fir trees near Black Sturgeon Lake that survived the budworm infestation. Five such trees were analyzed in detail by W. E. Cawthray, formerly of this laboratory, in connection with another project. Each of these trees had been producing crops of 50 to 125 cones at 2- or 3-year intervals for 10 to 20 years before the budworm outbreak, and all produced abundant crops in 1940. Yet 4 of these trees failed to produce another cone until 1951, while the fifth produced only a small crop in 1947. Balsam fir mortality generally exceeded 90 percent in stands throughout the Black Sturgeon Lake area, so that at best the seed production of these 5 survivors is representative of only a small fraction of the original forest. It is therefore not surprising that only a handful of seedlings apparently young enough to have completely post-dated the budworm outbreak were observed during the 1955 retally of these regeneration plots.

Height Growth of Balsam Fir Seedlings

At the time the height class samples were collected in 1951, all seedlings appeared superficially to be of recent origin. Height analysis, however, indicated that this vigorous appearance could be attributed to a few recent years of rapid growth, superimposed on the accumulated growth of many years of minute increments. A seedling typical of those collected in 1951 is illustrated in Figure 2. This seedling was collected near the Poshkakogan River, 20 miles north of Black Sturgeon Lake. Growth-ring examination at ground level indicated that this seedling had its origin in 1934, and yet in the 14 growing seasons up to the end of 1948 it had attained a height of only 15

inches. During the next 3 years, however, as overstory trees died, this seedling more than doubled its height by virtue of a sevenfold increase in its average annual growth rate. The branching of this seedling during its earlier growth suggests that its appearance before the death of the overstory was that of a low, sprawling shrub. The spirelike appearance of the more recent growth is somewhat accentuated by the killing of all but one of the 1949 terminal-lateral buds by a spring frost in 1950.

Growth curves calculated for seedlings collected throughout the Black Sturgeon Lake area gave an equally dramatic picture of this change in growth rate. Since the analysis of collections from any one plot showed this change in growth rate to have taken place in the same year on all seedlings, regardless of age or height, there could be no real doubt that this change reflected the release of the seedlings through overstory mortality. However, an even more convincing demonstration of the release phenomenon was provided by comparing the height growth of seedlings from devastated and undisturbed stands. Seedling collections for this comparison were made in the following manner. A group of 51 seedlings between 36 and 60 inches in height was collected in a stand near the Spruce River, the main inlet of Black Sturgeon Lake. All seedlings in this area showed a marked pattern of recently released growth, and for this area the history of overstory mortality was accurately known from other studies (Belyea, 1952). Control group "A" was collected in a healthy balsam fir stand near Kearn's Lake, 40 miles to the west of Black Sturgeon Lake and outside the limits of the budworm outbreak. This group of 27 seedlings was collected within the same height limits as the released group, so that its average height would be approximately the same. Control group "B" was composed of balsam fir seedlings growing beneath an extensive jack pine (*Pinus banksiana* Lamb.) stand at the north end of Black Sturgeon Lake. Although nearby balsam fir stands had suffered heavy mortality, the exposure of these seedlings beneath the jack pine overstory had remained unaltered. After analysis it was found that a combination of 38 seedlings that had occurred in the three 6-inch height classes between 30 and 48 inches had almost exactly the same average age as the released group from the Spruce River area. In this way two control groups were obtained from undisturbed stands: control group "A," selected for the same average height but expected to be appreciably older than the released seedlings, and control group "B," selected to have the same average age but expected to be appreciably shorter.

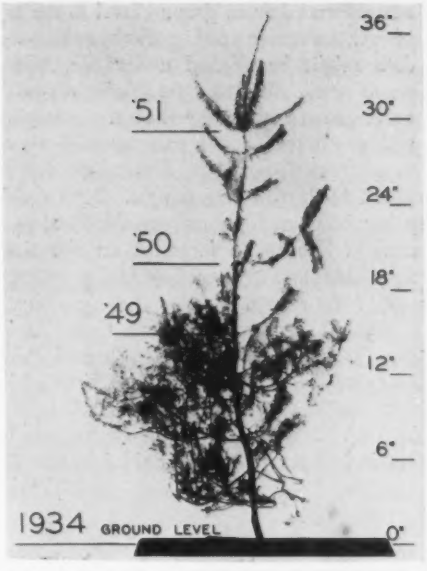

FIGURE 2. *Height growth of a balsam fir seedling during three growing seasons following release through death of overstory trees.*

A comparison of the growth curves for the two control groups and the released group is presented in Figure 3. In the preparation of this figure, height growth

was measured from ground level to the top of each successive year's growth, so that the data might be aligned under the appropriate years, and averaged to give a cumulative growth curve in one step. Averaging was continued in this manner so long as nodal growth could be determined for at least two-thirds of the sample. Beyond this point the growth curve was continued as a straight line to an intercept on the time scale abscissa corresponding to the average age of the group.

Several features of the growth curves in Figure 3 are noteworthy. Control "A" averaged 34 years of age, and reached in this time an average height of only 48 inches. This growth rate of approximately 1.4 inches per year is typical of balsam fir seedlings growing under severe suppression. Growing beneath a jack pine overstory, control group "B" reached an average height of 40 inches at an average age of 23 years, a growth rate only slightly better than that of control "A." The released group had reached a height of only 22 inches by 1948, and had at that time an average age of 18 years. Its growth rate up to that time had therefore been the poorest of the three, averaging only 1.2 inches per year. During the next 4 growing seasons, however, as overstory mortality climbed from 25 percent in 1948 to nearly 100 percent by 1951, these seedlings grew an additional 27 inches at a rate of approximately 6.7 inches per year. In this way these seedlings more than doubled, in 4 sea-

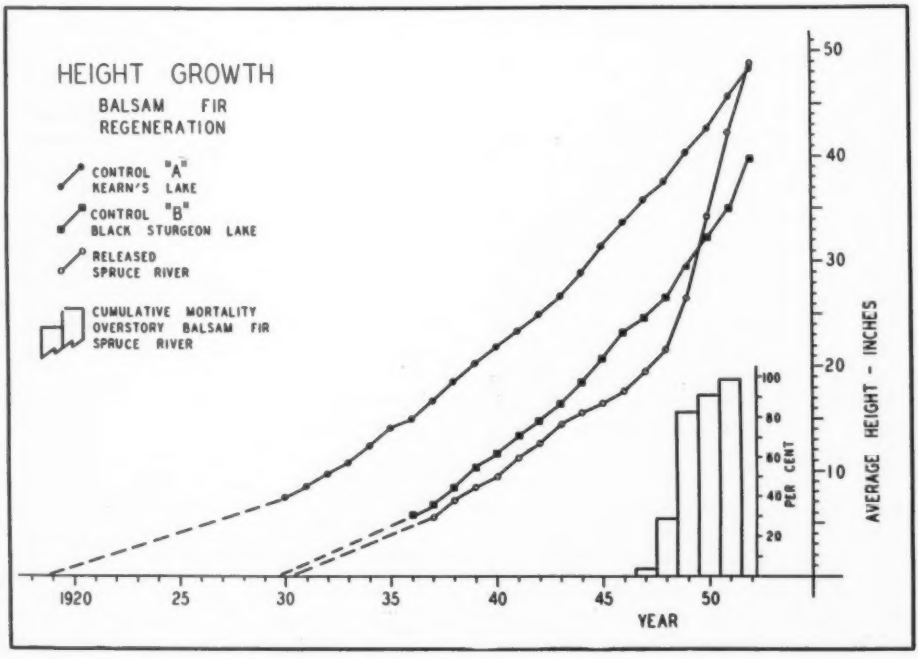

FIGURE 3. *Cumulative height growth of three groups of balsam fir seedlings. Control groups collected beneath undisturbed stands; released group collected beneath a budworm-killed balsam fir overstory for which the cumulative mortality histogram (from Belyea, 1952) is given in the lower right corner.*

sons of released growth, the height they had managed to attain in the previous 18 years. The slight decline in the growth rate of the released group between 1943 and 1947 can be attributed to the complete loss of many of the leaders through damage by late-instar spruce budworm larvae spinning down from the overstory.

The progress of overstory mortality for the Spruce River balsam fir overstory is given at the lower right in Figure 3 as a cumulative histogram (*from* Belyea, 1952). From this histogram it is apparent that overstory mortality took its biggest jump in 1949, and it is in this year that seedling height growth suddenly increased to a rate that surpassed all earlier years. Without the loss of many of the leaders through budworm feeding it is possible that height release would be manifested 3 or 4 years earlier during the period of heaviest overstory defoliation.

The growth curves in Figure 3 for the control groups, and particularly the curve for the older group from Kearn's Lake, are of interest for their own sake since they demonstrate the remarkable ability of balsam fir seedlings to tolerate conditions of suppression that permit only the most minute increments in annual growth. Morris (1948) has also noted this characteristic of balsam fir.

Terminal-Lateral Bud Number as a Criterion of Release

Suppressed seedlings produced only one or two terminal-lateral buds, and in extreme cases none at all. Vigorous, released seedlings on the other hand produced symmetrical groups of 3 to 5 terminal-lateral buds, up to 6 or 7. This suggested that terminal-lateral bud number might be directly correlated with shoot length. Both are products of contemporaneous tissue production and should be equally valid criteria for the release and improved vigor of the seedling. Such a correlation was found, and is depicted in Figure 4. The correlation coefficient of $+ .639 \pm .026$ expresses the relation between the 516 measurements of shoot length and terminal-lateral bud number presented in this figure. The square of this correlation coefficient indicates that approximately 40 percent of the variation in bud number is directly conjoined to variation in shoot length, though the causal mechanisms in this association lie outside the scope of this study.

It is concluded that the number of terminal-lateral buds and the length of shoot on which these are borne are simultaneous expressions of the vigor of balsam fir seedlings. It is likely that this is also true of other coniferous seedlings, though few other species are so tolerant of severe suppression as to present the same range of bud numbers for the assessment of this relationship.

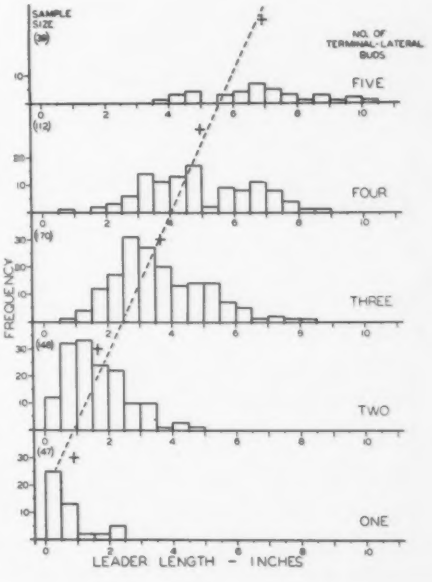

FIGURE 4. *Correlation diagram illustrating the relation found between 516 measurements of terminal-lateral bud number and shoot length.* $r_{xy} = + .639 \pm .026$.

FIGURE 5. *Typical seedling node distortion produced by spruce budworm feeding. Bud which has taken over as leader would normally have produced an internodal lateral branch.*

Evidence of Budworm History from Seedling Damage

During height-growth analysis a record was kept of the incidence of damage and distortion along the main axis of each seedling. Distortion of the main axis resulted either from the killing of the terminal or terminal-lateral buds before shoot elongation had started, or from defoliation and killing of the tip of the elongating shoot.

Examination of balsam fir seedlings in stands supporting high budworm populations on Sibley Peninsula in 1952 revealed that most of the seedlings were being fed upon by at least 1 or 2 larvae. At the time of examination, overstory defoliation was approaching 100 percent for the year, and the larvae had reached their later instars. Larvae feeding on balsam seedlings had evidently dropped from the nearly exhausted foliage of the overstory. The leaders of many of these seedlings were being attacked, suggesting that the photopositive reactions of the larvae, described by Wellington and Henson (1947), may have served to attract the larvae to the highest parts of the seedlings.

Figure 5 illustrates typical main-axis distortion. In this instance, both terminal and terminal-lateral buds have been destroyed. The bud which has taken over as the leader is one that would normally have developed into an internodal lateral branch. Subsequent diameter growth of the original leader appears to have been restricted to the lower portion that still forms a part of the main stem.

A comparison of the yearly incidence of such node distortion in seedling collections with overstory defoliation records from the same stands revealed satisfactory agreement. Seedling damage studies accurately portrayed the beginning and end of an outbreak, and indicated with moderate precision those years in which the budworm population had reached its highest levels. Figure 6 illustrates the agreement between the record of overstory defoliation at Muskrat Lake and the incidence of node distortion in a sample of 93 seedlings collected in the same locality. Here the record of seedling damage is more accurately portrayed for the declining years of the outbreak than for the years of population increase. This feature was characteristic of the seedling damage histograms for all plots, and may indicate a disproportionately low incidence of dropping larvae during the earlier years of an outbreak when overstory foliage is still abundantly available.

Similar studies near Chief Bay, Lake

Nipigon, indicated that a satisfactory history of an outbreak could still be obtained from the regeneration 5 years after the break-up of the overstory. In this area it was necessary to select seedlings partially shaded by shrub growth, since diameter growth had obscured the early nodal record of fully released seedlings. Careful selection with respect to diameter growth permitted node studies to be carried back 20 to 25 years, and there is no reason to suspect that any systematic sampling bias might have been incurred by the application of this criterion. It was also found advisable to restrict collections to seedlings that had attained a height of at least 18 inches at the time of the outbreak. Seedlings that had been shorter than this during known periods of heavy overstory defoliation rarely evidenced damage. Possibly these shorter seedlings are in some way protected or rendered less attractive by being merged with the ground vegetation.

Discontinuous nodal records often result from the complete killing of the upper portions of a seedling, with subsequent adventitious re-growth of a leader from the lower portion of the stem. Such seedlings must be discarded. Occasional distorted nodes should be expected in non-outbreak years, reflecting damage by other agencies such as animal browsing or frost. In short it is a technique that can be applied only with some caution, and in areas now under year-by-year surveillance for overstory defoliation it is clearly of no great value. However it is probable that in our more remote forested areas there will still be small outbreak centers that are not discovered until heavy defoliation and some mortality has occurred. In assessing the bioclimatological factors relevant to the development of such centers the technique may still prove of value in placing the early history of the budworm population on a reliable basis.

Seed Productivity of Balsam Fir Trees

In one study area near Black Sturgeon Lake an attempt was made to determine the seed production of the balsam fir component of a mixedwood stand. The stand selected was one in which aspen (*Populus tremuloides* Michx.) formed a dominant canopy, and accounted for 53 percent of the total basal area. Sub-dominant balsam fir was the next most abundant species, accounting for 29 percent. White spruce, black spruce, and balsam poplar (*Populus balsamifera* L.) made up the remaining 18 percent of the stand. Some of the balsam fir trees in this 70-year-old stand had been producing flowers for 37 years at the time of the study. This 37-year flowering period included many non-flowering years, and a break of 6 years during the period of spruce budworm defoliation when no female flowers were produced. Cruise figures for the stand indicated that there were 136 balsam fir trees per acre above 5 inches d.b.h. and that these had an average d.b.h. of 7.3 inches. Balsam firs 4 inches d.b.h. or less were not considered in the study, since no evidence could be found that they had ever produced female flowers.

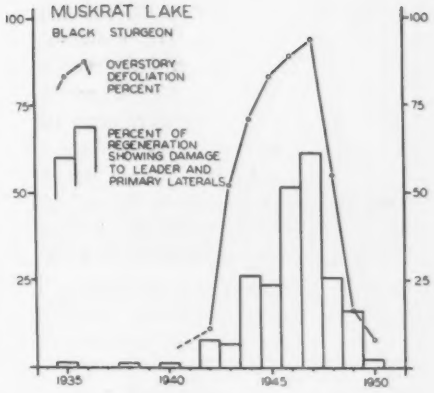

FIGURE 6. *Agreement between overstory defoliation and incidence of node distortion in a sample of 93 seedlings.*

Cone-spike counts were made on 9 trees distributed over the range of diameters from 5 to 11 inches. In analysis, these counts

were weighted by the occurrence of the various diameter classes in the stand, and in this way it was estimated that this stand produced approximately 59,000 cones per acre during the 37 years. Seed counts from 49 mature balsam cones indicated an average of 134 well-formed seeds per cone. From these figures it may be calculated that approximately 7,900,000 balsam fir seeds fell upon each acre of this forest during its 37 years of cone production. This total is equivalent to slightly less than 5 seeds per square foot of forest floor per year, a rate that does not seem illogically high when considered in relation to the very dense establishment of balsam seedlings occasionally observed in such favorable locations as the upper surface of rotten logs. These calculations did not include cones that appeared to have been harvested by red squirrels, and evidence from the cone spikes indicated that over half of the cones might have been so cropped in some years.

By 1952, this rate of seed production had effected an accumulation of 5,000 balsam fir seedlings per acre, most of which were less than 4 feet in height, although a few were as high as 6 feet. It would seem therefore that over this 37-year period only one seedling became established for every 1,500 seeds produced. A curious anomaly was presented by a comparison of the age distributions of the seedlings with the flowering history of the overstory. It appeared that in this area 67 percent of the seedlings established at the time of the study had originated during the first 19 years of the 37-year flowering history. Since only 28 percent of the total cone production took place during this same 19-year period, it may be inferred that in this stand early seed production was over twice as efficient in respect to seedling establishment as later seed production, one seedling becoming established for every 600 seeds produced during this earlier period. This observation suggests that the availability of seedling niches had begun to act as a limiting factor in seedling establishment after less than 20 years of seed production. The peak of efficiency in seedling establishment had evidently been passed when this stand was between 50 and 55 years of age—the period from 5 to 10 years before the outbreak of the spruce budworm.

Discussion

Through forest management it is reasonable to hope that we will someday effect a substantial reduction in the annual volume of insect-killed timber. Accordingly it is of the utmost importance to know whether a particular type of forest disturbance is liable to stimulate or repress seed production and seedling establishment. There is therefore a real need to study the history of seedling establishment in relation to forest disturbance whenever the opportunity presents itself. The observations of W. E. Cawthray, reported in this paper, indicate that among the earliest consequences of severe defoliation by the spruce budworm is the virtual cessation of balsam fir cone production. The situation is one in which, as Bess (1946) and Blais (1952) have shown, it is more correct to attribute the high populations of the insect to the flowering condition of the tree, than it is to attribute the flowering condition of the tree to the "distress" of insect defoliation.

Orchard pruning practices aim at the removal of whole branches that no longer adequately contribute to fruit production. In contrast it may be that insect attack, in producing a more uniform and severe destruction of the foliage itself throughout the crown, rarely if ever serves to stimulate flower production. In a recent paper Zivojinovic (1954) has recorded a distinct decrease in cone production by Austrian pine (*Pinus nigra* Arnold) in the Malyen mountains south of Belgrade as a consequence of heavy defoliation by *Diprion pini* (L.). Certainly present standards of evidence are such that the onus of proof should rest more firmly upon those who wish to make reference to "distress" seed crops following various forest catastrophes.

Taking together the data on age distributions of fir seedlings, and the data on their height growth under suppression, it becomes apparent that balsam fir presents an extreme picture of a species that reproduces itself by slowly accumulating its regeneration for many years, but under conditions that forbid these seedlings to replace the overstory until the overstory dies or is destroyed. The white spruce—balsam fir forest is perhaps rightly termed a "climax" forest, since it leads to no more advanced successional stages, and is capable of perpetuating itself, without first reverting to some more pioneer condition, by virtue of its ability to reproduce in its own shade. From the work of Blais (1954), which points up the long history of the spruce budworm as a harvester of mature balsam forests, and from the present study, we obtain a picture of a self-perpetuating but unstable climax forest that leads inevitably to periodic catastrophes under natural conditions. Such a climax might aptly be termed a "catastrophic climax."

The inference that the lack of suitable niches had begun to limit seedling establishment after less than 20 years of cone production suggests that the harvesting of balsam fir forests at the earliest economically feasible moment may entail relatively little sacrifice in seedling numbers. Thinking in terms of forest management practices that may someday anticipate the spruce budworm, we may come simply to associate the presence of an abundance of recently established balsam fir seedlings with the potential budworm susceptibility of the overstory. Flowering balsam fir is known to be outbreak-prone, and the presence of an adequate seedling population to replace the stand should offer a valuable criterion of the recent flowering history of the overstory. From the standpoint of forest management there is no need to wait for the prodigious seedling populations that will ultimately accumulate if the budworm does not in the meantime intervene.

Summary

1. Balsam fir seedlings present in the Black Sturgeon Lake forest area following the recent outbreak of the spruce budworm represented an accumulation of seedlings that had been building up for 20 to 30 years before the budworm infestation.
2. Studies of the flowering history of remnant survivors of the balsam fir overstory substantiated the conclusion based on seedling age studies that an early effect of defoliation was the cessation of female flower production.
3. During the pre-budworm period, shade-tolerant but severely suppressed balsam fir seedlings had grown at an average rate of just over 1 inch per year. Damage to seedling leaders by the feeding of late-instar larvae nullified any possible influence that concurrent overstory defoliation might have had upon seedling release. Height growth responded immediately, however, when the period of peak budworm populations had passed and heavy overstory mortality began.
4. Terminal-lateral bud number increased with increased leader length, and appears to be an equally valid criterion of seedling vigor.
5. Satisfactory histories of recent spruce budworm outbreaks can be obtained from the evidence of damage to the main axis of seedlings, caused by the feeding of late instar larvae that drop from the overstory. The beginning, end, and peak years of an outbreak are accurately portrayed.
6. Measurements of balsam fir seed productivity in a mixedwood stand indicated that nearly 8,000,000 seeds per acre had been produced over a 37-year flowering period. On the average, only 1 seedling became established for every 1,500 seeds produced. During the first half of this flowering period, however, 1 seedling became established for every 600 seeds produced, suggesting that

the availability of seedling niches quickly became a limiting factor in seedling establishment.

Literature Cited

BELYEA, R. M. 1952. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. II. An assessment of the role of associated insect species in the death of the severely weakened trees. J. For. 50: 729-738.

BESS, H. A. 1946. Staminate flowers and spruce budworm abundance. Dom. Dept. Agric. For. Ins. Invest. Bi-monthly Prog. Rept. 2: 3-4.

BLAIS, J. R. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana* Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). Can. J. Zool., 30: 1-29.

————. 1954. The recurrence of spruce budworm infestations in the past century in the Lac Seul area of northwestern Ontario. Ecology 35(1): 62-71.

DE GRYSE, J. J. 1944. Enemies of the forest—man or insects? Proc. Roy. Can. Instit. Ser. IIIA, Vol. IX, Sess. 1943-1944: 52-62.

GHENT, A. W., D. A. FRASER and J. B. THOMAS, 1957. Studies of regeneration in forest stands devastated by the spruce budworm. I. Evidence of trends in forest succession during the first decade following budworm devastation. For. Sci., 3: 184-208.

MORRIS, R. F. 1948. How old is a balsam tree? For. Chron. 24: 108-110.

WELLINGTON, W. G., and W. R. HENSON. 1947. Notes on the effects of physical factors on the spruce budworm, *Choristoneura fumiferana* (Clem.). Can. Ent., 79(9,10): 168-170.

ZIVOJINOVIC, S. 1954. The common pine sawfly in the Malyen. History of the outbreak and consequences of the defoliation of black pine. English résumé in Rev. App. Ent. 44(A)8: 278-279.

Respiration of White Pine Buds in Relation to Oxygen Availability and Moisture Content

BY
THEODORE T. KOZLOWSKI
ARTHUR C. GENTILE

POTENTIAL respiratory capacity of many internal plant tissues is not realized because diffusion of oxygen to these tissues is impeded by some physical barrier. MacDougal and Working (1933) and Chase (1934) have shown that oxygen tensions within tree stems are considerably different from those of the atmosphere. For this reason oxygen uptake of isolated stem sections is a better measure of respiratory capacity than of normal oxygen consumption in the intact tree (Goodwin and Goddard, 1940). Inhibition of oxygen uptake also commonly occurs in the interior of certain bulky fruits which carry on anaerobic respiration, at least in part, when insufficiently supplied with oxygen (Kidd, 1935). Another example of decreased aerobic respiration in internal tissues was cited by Pollock (1953), who found that tight scales of maple buds limited oxygen uptake of tissues within the bud.

No quantitative data are available to the authors on respiration of conifer buds before and after bud break or of effects of conifer bud scales on respiration of internal bud tissues. Such data should be of interest because of the structural differences between the relatively thick, fleshy bud scales of many hardwood species and thin, chaffy scales of conifer buds. The present investigation was initiated to study changes in oxygen uptake of pine buds from several weeks before until after bud break and to observe the effects of removal of bud scales on bud respiration during this interval.

Materials and Methods

In the spring of 1957 twigs of white pine (*Pinus Strobus* L.) were collected weekly from trees that averaged 16 in. d.b.h. at the state forest nursery, Amherst, Mass. Because of variations in bud development in different parts of the trees sampling was confined to twigs that had only one terminal bud and were on the lowermost whorls of branches. Twigs with terminal bud clusters were avoided to eliminate dealing with large variations in bud development between terminal buds and repressed laterals. Twig collections were made in the morning; immediately thereafter buds were carefully removed from the twigs in the laboratory and divided into two comparable groups.

Scales were removed from each bud in one of the two groups with the aid of forceps and a magnifying lens, care being taken to avoid injury to the young needle tissue within the bud. Equal numbers of buds with scales removed and of intact buds were floated overnight on tap water at

The authors are Professor and Head of the Department of Botany, Univ. of Massachusetts, Amherst, Mass., and Assistant Professor, respectively. Gratitude is expressed to Dr. P. J. Kramer and Dr. R. B. Livingston for reading the manuscript. The assistance of Mr. W. H. White is also gratefully acknowledged.

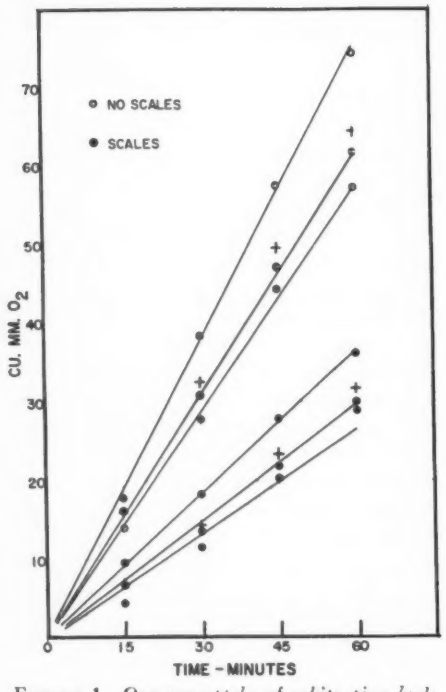

FIGURE 1. *Oxygen uptake of white pine buds with and without scales. Each line is fitted to data for one Warburg vessel containing 25 buds. The average values for buds with and without scales are indicated by (+). Data for April 11, 1957.*

room temperature (22°-25° C.) in separate beakers. The following morning buds of both groups were washed several times in distilled water and suspended in 3.0 ml. of 0.01M phosphate buffer, pH 7.1, in Warburg vessels. The center well of each vessel contained 0.2 ml. 20% KOH and a filter paper wick. Oxygen uptake was measured at 30° C. in a Warburg respirometer. Oxygen uptake of buds was determined simultaneously in six vessels; three contained intact buds and three contained buds with scales removed.

Early in the experiment 30 buds were placed in each vessel. Later in the season, as buds swelled, fewer were used, finally only 10 buds per vessel. After respiring in the vessels for 60 minutes the buds were removed, washed in distilled water, blotted dry and their fresh weights determined. Bud dry weights were also determined after oven drying at 90° C. for 24 hours. Rates of oxygen consumption were determined for buds collected at 7-day intervals beginning March 14 and ending after buds were fully opened. The final measurements were made on two successive days, May 1 and May 2, since all buds were not fully opened by May 1 but were opening rapidly. On May 2 buds were fully opened.

Results

Figure 1 shows a representative set of one day's data for oxygen uptake of dormant buds without scales and for intact dormant buds. Each straight line is fitted to data derived from respiring tissue in one Warburg vessel. The differences in slopes of the straight lines within each of the two groups may be attributed largely to normal differences between samples. The number of buds in each vessel was the same but there was some variation between vessels in fresh and dry weights of respiring material. Oxygen uptake at this time, prior to bud break, was essentially linear. An increased oxygen uptake by buds without scales over those with scales is apparent; that of buds without scales is more than twice that of buds with scales.

The results of a time-course study of respiration and moisture content of buds with and without scales are shown in Figure 2. Oxygen consumption, calculated on the basis of the amount taken up for each entire single bud, decreased in both groups from March 14 to March 21. After March 21 buds without scales showed a progressive increase in oxygen consumption until April 25, when they began to open, and then a large increase in oxygen uptake until they were fully opened. Intact buds, however, showed no real increase in oxygen consumption until April 25, when their rates suddenly increased greatly, and continued to increase until May 2 when mea-

surements were discontinued. Removal of scales resulted in consistently greater water uptake of buds, and rates of oxygen uptake in buds without scales were correspondingly higher. After bud break, the differences in moisture content of the two groups disappeared with time.

Respiration data for buds without scales and for intact buds are given in Figure 3 on both a dry weight and fresh weight basis. In terms of unit dry weight the removal of bud scales caused large increases in oxygen uptake of buds until the beginning of bud break when differences between the two groups began to decrease steadily. On April 18 respiration of buds without scales exceeded that of buds with scales by 313 percent; on April 25 by 163 percent; on May 1 by 41 percent; and on May 2 by 6 percent. When respiration data were computed on a fresh weight basis oxygen consumption of buds without scales showed no evidence of increase even after bud break. Intact buds did not increase their oxygen uptake appreciably until the beginning of bud break, and then showed a gradual increase.

Average fresh and dry weights of intact buds during the course of the experiment are given in Figure 4. The fresh weights represent data for buds after they were floated on water overnight and not the actual water content of buds on the trees. A slightly increased fresh weight shows up after March 21 with a much larger increase after bud break. Dry weights remained almost constant until April 18 when they began to increase steadily and were more than doubled within the next two weeks.

Figure 5 shows the relationship between oxygen consumption of buds and their moisture content expressed as percentage of dry weight of the tissue. The plotted values represent pooled data for buds with and without scales.

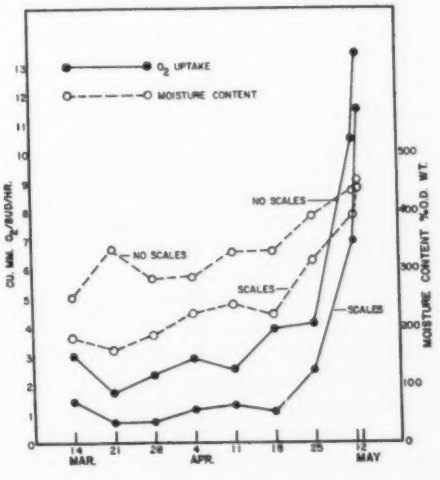

FIGURE 2. *Moisture content and oxygen uptake of white pine buds, with and without scales, from several weeks before until after bud break.*

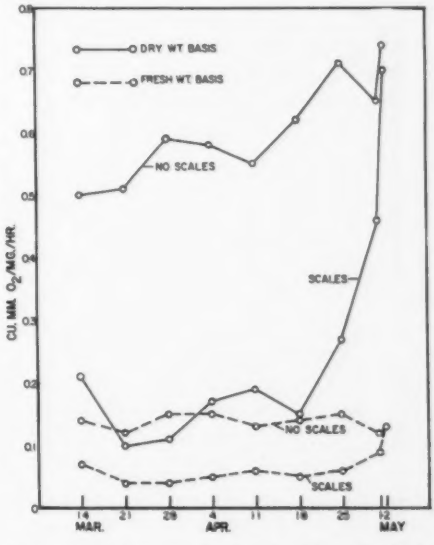

FIGURE 3. *Oxygen uptake of white pine buds, with and without scales, per unit of dry and fresh weight, from several weeks before until after bud break.*

Discussion

When computed on a dry weight or bud basis oxygen consumption of intact buds that were removed from lower branches of mature white pine trees was low until the time of bud break, when it increased rapidly. The lower rate of oxygen uptake of buds before bud break may be explained, at least in part, by the presence of bud scales which act as a physical barrier to diffusion of oxygen to internal respiring tissues. Pollock (1953) concluded that such an effect was operative in maple (*Acer*). In addition to this effect the present study emphasizes the important influence of moisture content of bud tissues on their rate of oxygen consumption.

Prior to the time of bud break, removal of bud scales significantly increased the capacity for oxygen uptake of buds. This increase was much greater on a unit dry weight basis than on a fresh weight or bud basis. After the time of bud break, as long as bases of scales continued to adhere to the newly-opened buds, oxygen uptake of intact buds was less than that of buds from which scales were removed. After bud break the differences in oxygen consumption between buds with scales and those without decreased rapidly until the scales dropped off.

Pollock (1953) concluded that oxygen uptake by intact maple buds was limited by the tightness of the bud scales, thickness of the individual scales, and permeability of the surface layers to oxygen. In the present study no measurements were made of respiration of individual scales because it seemed unlikely that the thin, chaffy scales of white pine buds would play a significant role, if any at all, in bud respiration. Structures of pine bud scales differ greatly from

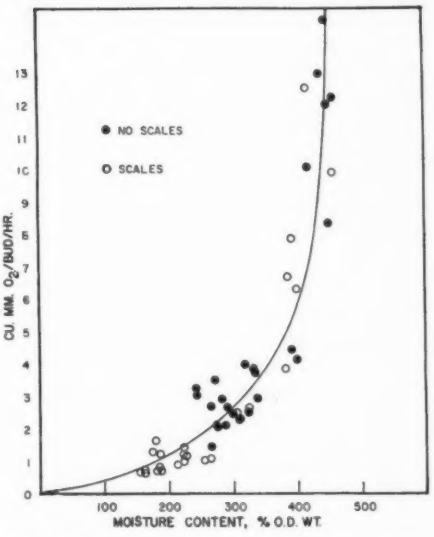

FIGURE 5. *Relation between moisture content and oxygen uptake of white pine buds both with and without scales. Data are for samples taken from several weeks before until after bud break.*

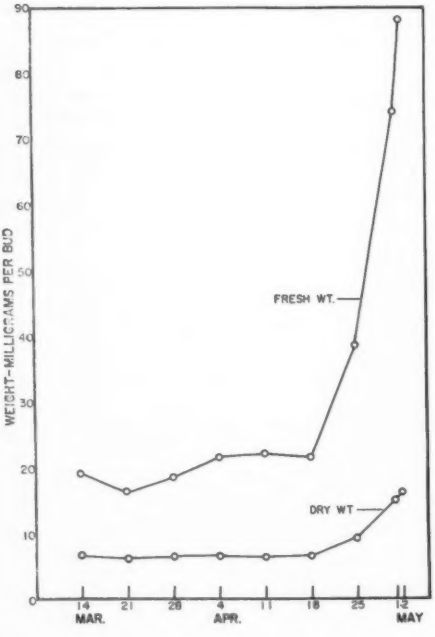

FIGURE 4. *Fresh and dry weights (after soaking for 24 hrs.) of intact white pine buds from several weeks before until after bud break.*

living bud scales of some broadleaved trees which can consume large amounts of oxygen. For example, Pollock (1953) found only 14 percent of total bud respiration in the growing point of Norway maple (*Acer platanoides* L.) buds and the remainder in the thick, fleshy bud scales. Thom (1951) found that in pear trees the outer bud scales are most active in respiration when the bud is young. He observed that young buds of pear trees consisted almost entirely of living tissues but when buds matured and outer scales thickened, some of the scale tissue died so only the base of outer scales was alive. Interior scales, however, were entirely living.

The failure of white pine buds with and without scales to show increased oxygen uptake with time on a fresh weight basis while they showed an increase on a dry weight basis suggested that: (1) buds without scales were absorbing water at a greater rate than were intact buds, and (2) oxygen consumption was influenced, at least in part, by moisture content of respiring tissues.

After bud break, moisture contents of samples with and without scales came together with time and so did their respiration rates. Considering intact buds only, there is also correlation with hydration of tissues because their rates of oxygen consumption were rather constant until the time of bud break. They then went up rapidly as did their moisture contents. Furthermore, when respiration rates for both groups were plotted over moisture content a close relationship between tissue hydration and oxygen uptake was evident for the pooled data (Fig. 5). Although Pollock (1953) did not stress the importance of water relations in bud respiration, the present study indicates that they should be carefully considered. The technique of floating tissue sections on water prior to manometric determinations should be evaluated as a factor which influences oxygen uptake of the tissues studied. Although the large increases in moisture content of buds with scales removed over intact buds were brought about artificially by floating buds on water, nevertheless a clear correlation between moisture content and oxygen uptake was shown. This suggests that respiration of buds on trees is also affected by their moisture content. However, more data are needed on variations in moisture contents of buds on trees before generalizations can be made about the relative importance of moisture content in controlling bud respiration under natural conditions.

Increased respiration of buds after bud break may also be partly attributed to increased amounts of respiratory substrate. Dry weight increase of intact buds showed little change from week to week until buds burst, but then it increased rapidly. The rapid dry weight increase after bud break probably resulted from excess of synthesized carbohydrates over respiratory loss and from materials translocated into the expanding buds. Translocation of organic materials and minerals in to buds prior to bud break may have masked any real consumption of reserves by respiration. Gäumann (1935) found that in beech (*Fagus*) trees translocation of organic reserves from twigs into buds from January until bud break exceeded the respiratory deficit.

Summary

1. Oxygen uptake, fresh weight, and dry weight of white pine buds, with and without scales, were measured from several weeks before until after the time of bud break.

2. Oxygen uptake, fresh weight, and dry weight of intact buds were low until the time of bud break, when they increased rapidly. Oxygen uptake of buds with scales removed was signficantly greater than that of intact buds but this difference decreased rapidly after bud break.

3. Oxygen uptake of white pine buds appears to be limited by availability of oxygen to internal bud tissues and by moisture content of respiring cells. The degree to which either of these limiting factors inde-

pendently affected respiration could not be determined from the present experiments.

Literature Cited

CHASE, W. W. 1934. The composition, quantity, and physiological significance of gases in tree stems. Minn. Sta. Tech. Bull. 99.

GÄUMANN, E. 1935. Über den Stoffhaushalt der Buche (*Fagus silvatica* L.) Ber. der deut. bot. Gesell. 53: 366-377.

GOODWIN, R. H. and D. R. GODDARD. 1940. The oxygen consumption of isolated woody tissues. Amer. J. Bot. 27: 234-237.

KIDD, F. L. 1935. Respiration of fruits. Nature 135:327-330.

MACDOUGAL, D. T. and E. B. WORKING. 1933. The pneumatic system of plants, especially trees. Carnegie Inst. Wash. Publ. 441: 1-87.

POLLOCK, B. M. 1953. The respiration of Acer buds in relation to the inception and termination of the winter rest. Physiol. Plantarum 6:47-64.

THOM, A. L. 1951. A study of the respiration of hardy pear buds in relation to rest period. Ph.D. dissertation Univ. of Calif. Berkeley.

Identification of Living Gymnosperms on the Basis of Xylotomy

By Dr. Pál Greguss. 720 pp. Illus. Akadémiai Budapest. 1955. $14.00.

Review by E. S. Harrar,
Duke University,
Durham, North Carolina

This tome, composed on 9" x 13" pages, is an English translation by Mrs. L. Jocsik of the author's original Hungarian manuscript. It embraces 263 pages of text, more than 350 full-page plates combining half-tone photomicrographs and line-cut drawings depicting the anatomical structures of the wood of 352 species of the *Gymnospermae*, a bibliography of 171 references the majority of which are of European origin, and an index. Several tabular summaries delineating the xylotomical features of all known genera of gymnosperms together with similar but more detailed charts for the species of each group that the author was privileged to examine, are to be found in a pocket provided on the inner face of the back cover.

The preparation of this volume is indeed an expression of the labors of love, and the climax to many years of painstaking and time-consuming effort. The author was not only faced with the prodigious task of assembling a large collection of authentic specimens of wood from the forested regions of the world, but also with the stupendous job of cutting and mounting thousands of thin sections suitable for preparing his anatomical analyses, photomicrographs, and drawings.

The text material is divided into two major sections which the author titles "General Part" and "Circumstantial Part," respectively. The former deals with histological techniques and the anatomical characteristics of gymnospermous wood *per se*. Of possible interest to all

researchers concerned with the microtechnique of woody tissue is a carbonization process which was employed in preparing the sections for microscopic study and which eliminates the need for time-consuming staining schedules. The remainder of this "Part" dwells at length with phylogenetic considerations.

Included under the heading "Circumstantial Part" are nine analytic keys leading to the identification of species within the various family and generic groups, and very detailed anatomical descriptions of the wood of each of the 352 species considered.

The volume is much more than a compendium of anatomical data for gymnospermous timbers. The author has also endeavored to develop a phylogenetic system of classification for the various groups based in large measure upon the complexity of structure of the wood rays and tracheids, and correlated with appropriate morphological features of the plants themselves. In his brief summary in defense of his system he states:

"The xylotomical findings of the present writer lead him to the conclusion that on the evidence of ray structure of their members, the 9 or 7 existing families of the *Gymnospermae* and *Coniferae*, respectively, can be divided into three fairly well circumscribed evolutionary series, each of which shows phyletic correlations with one of the three types of the *Pteridophyta*, viz: 1. *Cycas*, *Ginkgo*, *Araucariaceae*, *Podocarpaceae*, and *Taxales* with the *Pteropisda*; 2. *Cupressaceae* with the *Sphenopisda*; 3. *Taxodiaceae* and *Pinaceae* with the *Lycopsida*. All this makes it probable that the *Gymnospermae*, including the *Coniferae*, are, like the *Pteridophyta*, not of monophyletic but at least triphyletic origin."

In the opinion of certain European referees this rather novel conception is of an individual character and one which they are unable to accept, a view also held by this reviewer.

The photomicrographs in the pictorial section of this book are only fair to good. Many of the cell-wall sculpturings are obscured by shadows or ruptures developed in sectioning. Some few appeared to have been made from sections too thick for good photomicrographic work. On the other hand, the drawings which accompany the half-tones are excellent in their every detail, and collectively, are without doubt one of the finest assemblies of their kind.

The book contains many misspellings, which, in the case of scientific names is most unfortunate, and inexcusable. An occasional German word has also found its way into the text material. Nevertheless, this is an authoritative piece of work and contains a wealth of anatomical material pertaining not only to the gymnosperms as a group, but also to several little known genera and species. Wood anatomists having particular interest in conifers will do well to become familiar with its contents.

Proliferated Cones of Douglas-Fir

BY
WILLIAM S. LOONEY
JOHN W. DUFFIELD

THE CONE-COLLECTING crew of the Simpson Olympic Tree Farm in the autumn of 1957 came upon a young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), which bore an appreciable crop of proliferated cones. The tree, 35 feet tall, 10 in. d.b.h. and 20 years old, is located in the Wynooche valley, about six miles southwest of Camp Grisdale, Grays Harbor County, Washington.

Although proliferation of Douglas-fir cones is not rare, this case is of special interest. One or a few proliferated cones may be found on trees which bear large numbers of normal cones. In this instance, however, all the cones on the tree were proliferated, suggesting that the proliferation is conditioned by a gene or genes with high penetrance.

The gross features of a typical proliferated cone differ from a normal cone in several respects (Fig. 1). First, the cone is markedly pedunculate, whereas the normal Douglas-fir cone is essentially sessile. Second, the bracts and ovuliferous scales increase rather gradually in size at the (indistinct) base of the cone. Third, the bracts remain green long after the scales have become dry and brown and have opened appreciably. Fourth, the apex of the cone terminates with a cluster of bracts which extend well beyond the apical scales.

Figure 2 shows a dissection of a proliferated cone. At the upper left is a normal needle, in the axil of which the proliferated cone was produced. Next comes an essentially normal bud scale, such as can be found at the base of a normal cone. Next a series of four bracts, which become progressively less needle-like and more bract-like. Then, alternately, are ovuliferous scales and bracts showing their progressive

FIGURE 1. *Proliferated cone, showing long "peduncle" and three-pointed bracts subtending cone.*

The authors are respectively Forester, Simpson Olympic Tree Farm, Shelton, Washington, and Technical Director, Col. W. B. Greeley Forest Nursery, Nisqually, Washington.

modification up the stem. Finally, the apical portion of the stem or cone-axis showing a tuft of needle-like bracts. Not all the bracts and scales from the cone are included in this figure. No fully-developed seed were produced by this cone, nor on the entire tree.

Proliferated cones are not uncommon among the conifers. Chamberlain,[1] among others, discusses this phenomenon and gives illustrations. The morphological significance of proliferated cones is that they support the theory that the conifer cone is a modified, complex shoot.

The tree reported here will be saved and vegetatively propagated for further study.

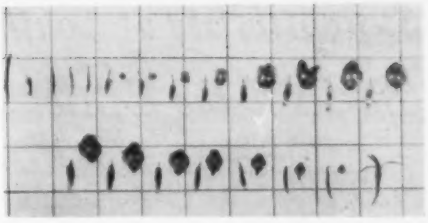

FIGURE 2. *Dissection of proliferated cone. Upper left, normal needle subtending cone "peduncle." Next right, normal bud scale. Next, a series of four bracts which become increasingly three-pointed. Then alternating scales and bracts, and, lower right, the apex of the cone axis, terminating in a tuft of bracts.*

[1]Chamberlain, C. J. 1935. Gymnosperms. Structure and evolution. Univ. of Chicago Press. Chicago.

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Susceptibility of Southern Pines and Other Species to the Littleleaf Pathogen in Liquid Culture

BY
BRATISLAV ZAK
WILLIAM A. CAMPBELL

RECENT STUDIES ON THE CAUSE of littleleaf have been reported by Campbell and Copeland (1954). This widespread disease of pine in the Piedmont of the Southeast develops as the root systems of affected trees become gradually restricted from periodic killing of extending and short root tips by the soil fungus, *Phytophthora cinnamomi* Rands. Adverse soil conditions such as poor drainage and aeration, low fertility, and periodic moisture stress contribute to the gradual decline of diseased trees and the condition known as littleleaf.

In the course of investigations on the cause of littleleaf, the root systems of shortleaf pine (*Pinus echinata* Mill.) and loblolly pine (*P. taeda* L.) seedlings were exposed to attack by *Phytophthora cinnamomi* both in soil and in liquid solution cultures. Some of this work has been briefly reported by Campbell and Copeland (1954). This paper presents a more detailed account of inoculations made in liquid culture including the testing of species other than shortleaf and loblolly pine.

One of the studies tested the difference in susceptibility of shortleaf and loblolly pine to attack by *P. cinnamomi*. A second study exposed roots of these two pine species plus those of slash pine (*Pinus elliottii* var. *elliottii*), longleaf pine (*P. palustris* Mill.), Arizona cypress (*Cupressus arizonica* Greene), sweetgum (*Liquidambar styraciflua* L.), and redbud (*Cercis canadensis* L.) to attack by this fungus to determine other possible hosts.

Materials and Methods

One-year-old, nursery-grown seedlings of shortleaf and loblolly pine were placed in commercial "Hyponex"[1] nutrient solution, adjusted to approximately pH 5.5 by the addition of dilute acetic acid, in late November. Each culture was continuously aerated by a slow stream of air bubbling through the solution. Temperature was not manipulated beyond maintenance of greenhouse air temperatures between 15° and 25° C.

Two months later, the seedlings with newly developed roots were transferred to a water-soil medium in 2-gallon glazed crocks. The medium was prepared by mixing 40 grams of air-dry Norfolk fine sand with each 2 gallons of water. After 24

[1]Hydroponic Chemical Co., Inc., Copley, Ohio.

The authors are Pathologists, Southeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture. They are stationed at Athens, Ga. Project in cooperation with the School of Forestry, University of Georgia.

hours, when the mixture had cleared, the seedlings were removed from the nutrient solution, rinsed in tap water, and placed in the new medium. They were supported in large cork stoppers inserted in holes in an asbestos sheet covering each container.

Eight crocks were used, each with 10 seedlings, five loblolly and five shortleaf pine, or a total of 40 seedlings of each species. Four of the crocks were aerated with compressed air and four were not aerated. A split-plot type of randomized block design was employed.

Inoculum of *Phytophthora cinnamomi* was prepared as follows: Cooked wheat grains were placed in 1-pint Mason jars fitted with special tops for inoculation and sterilized. When cool, the wheat was inoculated from fresh cornmeal agar cultures of *P. cinnamomi* isolated from soil by Campbell's (1949) technique. After 2 months, when each wheat grain was permeated with mycelium, two level teaspoons of the inoculum were placed in a small cheesecloth sack with a few glass beads for ballast. Enough sacks of inoculum were prepared to provide two per crock.

These sacks were then suspended 4 inches below the surface in a water-soil mixture as previously described. After 24 hours, a number of wheat grains were removed and examined for the characteristic asexual fruiting bodies of the fungus. When numerous zoosporangia were observed growing from the surfaces of the grain, two sacks of inoculum were placed 4 inches below the surface in each crock containing the seedlings.

Four days later, one seedling of each species was removed from each crock for examination. The roots were rinsed in tap water and about 12 root sections were severed from each and placed on cornmeal agar for detection of *P. cinnamomi*. The root sections consisted of root tips 1 centimeter in length, and root pieces 2 centimeters in length taken directly back of the tip section. After 24 hours, the plated root sections were examined microscopically for outgrowth of the easily recognizable mycelium of *P. cinnamomi* and data recorded. Each day, thereafter, another set of seedlings was removed from the water-soil medium and the roots plated. On the sixth day one set was cultured in the morning and another in the late afternoon. The last set was removed on the seventh day.

In the second study, roots of shortleaf, loblolly, slash, and longleaf pine, as well as Arizona cypress, sweetgum, and redbud were exposed to attack by *P. cinnamomi* in liquid culture. Two- to 4-month-old seedlings of each species were grown for one month in Hyponex nutrient solution adjusted to pH 5.2 and maintained at approximately 23°C. by use of a refrigerated water bath. The seedlings were randomly distributed among 4 glazed, 2-gallon crocks each fitted with aerators. Seventy-six hours after inoculation, all seedlings were removed from the crocks and their roots gently rinsed in running tap water. Following this, as many root tips as possible were severed from each and placed in covered Petri dishes containing 5 mm. of tap water at approximately 25°C. At the end of 12 hours, all root tips were examined microscopically within an hour for outgrowth of zoosporangia of *P. cinnamomi* (Figs. 1 and 2) and the data recorded.

Results

Shortleaf versus loblolly pine. Infection of roots based on recovery of *P. cinnamomi* after plating was first observed on the third day after inoculation, and systematic samplings began on the fourth and extended to the end of the seventh day. The results of this day-to-day sampling are given in Figure 3. Infection of roots of both species increased to a maximum 6½ days after inoculation and then dropped sharply. The roots of shortleaf pine were consistently more heavily attacked than were those of loblolly pine.

The results of this study may be further examined in Table 1, which lists by root tips, root pieces, and both combined the percent of shortleaf and loblolly roots in-

FIGURE 1. *Zoosporangia of* Phytophthora cinnamomi *emerging from root tip of shortleaf pine seedling grown and inoculated in liquid culture.*

fected. No difference was apparent between the aerated and nonaerated series, so these data were combined in Table 1. The data for root sections, including that for root tips and pieces, were analyzed statistically by first making the transformation arc sin $\sqrt{\text{percentage}}$. In all, 385 root sections of shortleaf pine were examined, and of them 58 percent were infected with *P. cinnamomi.* Only 39 percent of 457 loblolly pine root sections were attacked. This difference between the two species is statistically significant at almost the 1-percent level.

Other species. Table 2 lists the other species tested for susceptibility to attack by *P. cinnamomi.* The roots of all four pine species were heavily attacked. Those of Arizona cypress and redbud were slightly affected. Only the roots of sweetgum appeared to have completely escaped attack by the pathogen.

Discussion

Field surveys clearly indicate that shortleaf pine is more susceptible than loblolly pine to littleleaf. A 5-year record of littleleaf by Roth, Buchanan, and Hepting (1948) on 31 plots established throughout the range of the disease showed that 10 percent of the

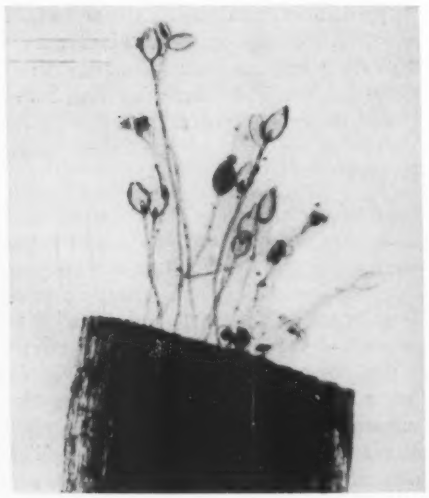

FIGURE 2. *Zoosporangia of* Phytophthora cinnamomi *growing from cut surface, 5 mm. back of tip, of shortleaf pine seedling root 12 hr. after severing. Tree was grown in liquid culture and inoculation made 3 days before cutting root.*

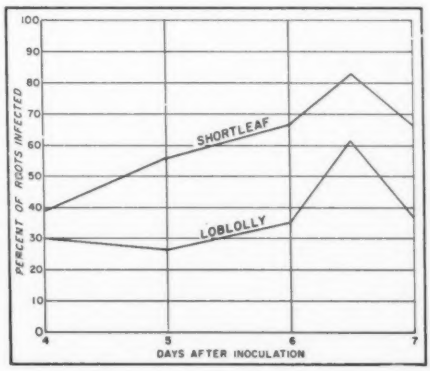

FIGURE 3. *Daily percent of roots of shortleaf and loblolly pine seedlings in liquid medium infected, based upon recovery of* P. cinnamomi *after plating. The sudden drop on the seventh day for both species suggests secondary invasion by other organisms which probably suppressed* P. cinnamomi *when root sections were plated.*

TABLE 1. Infection of roots of shortleaf and loblolly pine seedlings by P. cinnamomi *in liquid medium over a 7-day period.*

Species	Seedlings tested	Seedlings with roots attacked by *P. cinnamomi*	Root tips examined[1]		Root pieces examined[2]		All root sections examined	
			Total	Infected	Total	Infected	Total	Infected[3]
	Number	*Number*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Pinus echinata	38	38	299	61	86	48	385	58
Pinus taeda	40	37	348	44	99	24	457	39

[1]Severed 1 centimeter back of root cap.
[2]Two-centimeter section back of tip piece.
[3]Difference between species is statistically significant at almost 1-percent level.

shortleaf and only 3 percent of the loblolly pine died. In another survey by Copeland (1952) made in the South Carolina Piedmont, it was found that 13 percent of the shortleaf and 3 percent of the loblolly pine were affected by littleleaf.

This difference in littleleaf susceptibility must be related to a differential response by the two species to one or more of the factors contributing to this disease. These include the infection and killing of root tips by the fungus *Phytophthora cinnamomi*, and adverse soil conditions such as poor drainage and aeration, low fertility, and inadequate moisture, which tend to lower the vigor of the tree.

Results of the first portion of this study help explain part of the difference in susceptibility of the two species to littleleaf. Roots of both were rather heavily attacked by the pathogen, but about 1½ times more root sections of shortleaf pine were infected by *P. cinnamomi*.

However, this difference is far short of that suggested by the field surveys which indicate that shortleaf is 3 to 4 times more susceptible to littleleaf than loblolly pine. To gain a more complete understanding of this inequality one must obviously examine the remainder of the causal complex of this disease. One study by the senior author[2] indicates that shortleaf is much less tolerant than loblolly pine to poor soil aeration.

Part of the higher resistance to littleleaf of loblolly pine may be due to the inherently greater vigor of the species. The actual damage to the root system by *P. cinnamomi* is confined primarily to the tips of extending and short roots. Most of the infection and killing of roots occurs in early spring and in mid-autumn when new rot tips are formed and soil moisture and temperature are favorable for the pathogen. If the tree can regenerate sufficient new roots after each attack to avoid a gradual decline, littleleaf symptons may be averted. This ability to regenerate new roots is dependent on the vigor of the tree as modified by site conditions.

The other species attacked in liquid cul-

TABLE 2. Infection of roots of pines and other woody species by P. cinnamomi *in liquid medium.*

Species	Trees tested	Root tips examined	
		Total	Infected with *P. cinnamomi*
	Number	*Number*	*Number*	*Percent*
Pinus echinata	2	64	59	92
Pinus taeda	4	80	46	58
Pinus palustris	4	87	56	64
Pinus elliottii var. *elliottii*	4	61	33	54
Cupressus arizonica	2	65	15	23
Cercis canadensis	2	62	4	7
Liquidambar styraciflua	2	83	0	0

[2]Zak, B. Importance of soil aeration and other factors in the littleleaf disease of shortleaf and loblolly pine. Unpublished thesis, Duke University, 180 pp. 1954.

ture by *P. cinnamomi*, listed in Table 2, lend further support to the world-wide reputation of this plant parasite. Among its hosts are both native and introduced species of woody and herbaceous plants. In this country it has been associated with a destructive root rot of American chestnut (*Castanea dentata* (Marsh.) Borkh.), which caused heavy mortality in chestnut in the Southeast long before the appearance of the blight (Crandall, Gravatt, and Ryan, 1945). It is still abundant in the soils of the Piedmont of the Southeast but now associated with a pine root disease.

Slash and longleaf pine roots in liquid culture appear to be quite susceptible to attack by *P. cinnamomi*. Both escape injury from littleleaf because the Coastal Plain soils in which they grow lack conditions requisite for development of the disease. However, in certain sections of Alabama and Georgia where the range of longleaf pine extends into areas of heavier soils and into the range of shortleaf and loblolly pine, a littleleaf-like condition of this species may occasionally be seen, especially on severe littleleaf sites.

Both redbud and sweetgum commonly occur in association with shortleaf and loblolly pine on littleleaf areas. Of these two species, only redbud was mildly attacked by *P. cinnamomi* in liquid culture. It is likely, considering the omnivorous character of this pathogen, that other woody and even herbaceous vegetation on littleleaf sites is also attacked in varying degrees.

The results of these tests must be interpreted with the understanding that the growth and inoculation medium was a liquid and not soil. The roots formed were non-mycorrhizal and lacked suberization. Nevertheless, the study does indicate the relative susceptibility of the basic root tissue of the various species to attack by *P. cinnamomi*. The differences indicated are probably inherent differences in susceptibility between species. Further inoculation tests in soil must be made to determine whether species other than shortleaf and loblolly pine are normally hosts for this soil-borne fungus.

Summary

Two liquid culture inoculation studies made during investigations on the littleleaf disease of pine are reported. Seedling roots of several coniferous and broadleaf species were tested for relative susceptibility to attack by the soil-borne fungus *Phytophthora cinnamomi*.

The first study determined the difference in susceptibility of roots of shortleaf and loblolly pine seedlings when subjected to attack by zoospores of *P. cinnamomi*. Shortleaf pine roots were significantly more susceptible: 58 percent of root sections of this species were infected over a 7-day period as compared to 39 percent of those of loblolly pine. This difference between the two species explains in part why shortleaf is much more susceptible to littleleaf than loblolly.

The second study determined the relative susceptibility to attack by *P. cinnamomi* of roots of shortleaf, loblolly, slash, and longleaf pine and those of Arizona cypress, sweetgum, and redbud. Roots of all four pine species were heavily attacked. Those of Arizona cypress and redbud were lightly affected. Only sweetgum escaped without damage to its root system.

Literature Cited

Campbell, W. A. 1949. A method of isolating *Phytophthora cinnamomi* directly from soil. U. S. Bur. Pl. Ind., Plant Dis. Reptr. 33: 134-135.

———— and O. L. Copeland, Jr. 1954. Littleleaf disease of shortleaf and loblolly pines. U. S. Dept. Agric. Cir. 940. 41 pp., illus.

Copeland, O. L., Jr. 1952. Root mortality of shortleaf and loblolly pine in relation to soils and littleleaf disease. J. For. 50: 21-25.

Crandall, B. S., G. F. Gravatt, and M. M. Ryan. 1945. Root diseases of Castanea species and some coniferous and

broadleaf nursery stocks, caused by *Phytophthora cinnamomi*. Phytopathology 35: 162-180.

ROTH, E. R., T. S. BUCHANAN, and G. H. HEPTING. 1948. A five-year record of littleleaf on thirty-one plots. U. S. Bur. Pl. Ind., For. Path. Spec. Release 32, 9 pp., illus.

Variation in Tracheid Length and Wood Density in Geographic Races of Scotch Pine

By Robert M. Echols. Yale University School of Forestry, New Haven, Conn. Bul. No. 64, 52 pp., illus. 1958. $1.50.

Review by W. T. Doolittle,
Forest Service, U. S. Department of Agriculture

This bulletin, a published version of Dr. Echols' doctoral dissertation presented to the Yale School of Forestry, deals with the relationship of wood properties to environment and genetics.

Scotch pine (*Pinus sylvestris* L.) is probably the most widely planted of forest trees introduced in the United States, and its importance continues to grow because of its hardiness and utility. The present study relates tracheid length and wood density to 15 geographic races from Latitudes 45 to 70 in western Europe planted in 1938 on the Fox State Forest near Hillsboro, New Hampshire.

Sweden's O. Langlet has stated that the following differences between various Scotch pine provenances have proven to be hereditary: resistance to attacks of pine scab; annual growing period (length); rapidity of growth; size, color, and winter coloration of the needles; stem shape; phototropism in seedlings; and dry-matter content of the needles in autumn. Echols' study shows two additional properties to be hereditary—tracheid length and wood density. The latitude of provenances was highly correlated with tracheid length, tree height, bark thickness, d.b.h., and wood density. Other interesting correlations found were between wood density and d.b.h., width of growth ring and tracheid length, wood density and tracheid length, and tree height and tracheid length.

The work is probably most important because of the implications of similar relationships of wood properties for other species. Another more immediate and practical use of the results of this study will be to serve as a guide to New England foresters in choosing Scotch pine sources for specific purpose, e.g., fast growth, high-wood density, or long tracheids. The author also suggests that it may be possible to predict the height growth of older trees by sampling the length of tracheids in seedlings. It is hoped that the results of this study will stimulate further biological investigations of Scotch pine and other species.

Site-Quality Relationships of Pine Forests In Southern Arkansas and Northern Louisiana

BY
ROBERT ZAHNER

EFFICIENT FOREST MANAGEMENT in many parts of the country today requires site classification of timberland. Large expenditures for forest development are fully warranted on good sites. Often, however, blanket treatments are applied to the area as a whole, with little regard for the productive capacity of individual acres within the forest. With intensification of forest management has come the need for acre-by-acre classification of site quality.

While several studies have correlated soil and topography with growth of southern pines, such studies have been confined to limited areas, and their results have not necessarily been adaptable elsewhere. The present study attempted to obtain basic data from which to develop a method for evaluating site quality for loblolly and shortleaf pines (*Pinus taeda* L. and *P. echinata* Mill.) on upland and terrace soils in southern Arkansas and northern Louisiana. A field guide for practical application of this study has been published (Zahner, 1957).

Background

Billings (1952), Heiberg and White (1956), and others have stressed the complexity of the factors affecting growth. In practice it is impossible to evaluate the whole environment, but certain effective or limiting factors can be studied, and their relation to growth evaluated.

Two soil factors that limit southern pine growth at times during each growing season are soil moisture and soil aeration (Barnes and Ralston, 1955; Coile, 1935, 1948, 1952; Coile and Schumacher, 1953; Dingle and Burns, 1954; Gaiser, 1950; Goggins, 1951; McClurkin, 1953; Metz, 1950; Ralston, 1951; Turner, 1938; Zahner, 1954). Soil moisture and aeration are often difficult to measure directly in the field, and most investigators evaluate them indirectly, through physical features of topography and the soil profile.

Topography, measured by surface drainage, is associated with site quality of loblolly pine in the Atlantic and Gulf Coastal Plain (Gaiser, 1950; Metz, 1950; Zahner, 1954). Site index (height in feet 50 years after seed germination) is reported to increase with decreasing surface drainage, reflecting site changes from slopes to the generally moister flatwoods.

The effect of depth to subsoil, or the thickness of the surface horizon, has also received much attention (Coile, 1935, 1948; Coile and Schumacher, 1953; Dingle and Burns, 1954; Gaiser, 1950; Goggins, 1951; Metz, 1950; Zahner, 1954). Site index for both loblolly and shortleaf pines consistently increases with increasing surface soil thickness. It has been suggested that this factor is a measure of the well-aerated space for root development above

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more restrictive subsoils (Coile, 1952).

For the shallow surface soils of the Piedmont, Coile (1948) reported the depth-site index relationship to be curvilinear, i.e., increments of thickness improved site quality more on very shallow soils (less than 6 inches thick) than on moderately deep soils (from 12 to 18 inches thick). Metz (1950) and Zahner (1954), working in Coastal Plain regions where surface soils are rarely shallow, found the relationship to be linear, with site index increasing steadily as surface soils increased from 6 to 24 inches.

The physical characteristics of the subsoil, as they regulate water movement, water retention, and soil aeration, have long been known to be associated with site quality for loblolly and shortleaf pines. Early linear correlations with clay and silt-plus-clay contents were partially successful (Coile, 1935; Turner, 1938), and site index was found to decrease with increasing subsoil fines. Later investigations found better correlations with other subsoil properties, among them the imbibitional water value (Coile, 1948; Coile and Schumacher, 1953; Gaiser, 1950; Metz, 1950; Zahner, 1954).

Coile (1948), and later Coile and Schumacher (1953), found that site index decreased linearly with increasing imbibitional water values in heavy Piedmont subsoils. This relationship was attributed to poorer soil aeration in subsoils with high values of imbibitional water.

Gaiser (1950) and Metz (1950), both working with relatively light subsoils in the Atlantic Coastal Plain, reported that site index increased with increasing values of imbibitional water. They found curvilinear relationships, with site index leveling off at moderately high values of imbibitional water. This seeming contradition to Coile's findings is partially explained by the fact that while Coile measured changes from light clays to heavy clays, Gaiser and Metz measured changes from sands to relatively light clays. Thus, their findings reflected increasing site index with increasing moisture conditions. This matter is further reviewed in a later paper by Gaiser (1951).

In the west Gulf Coastal Plain, Zahner (1954) found that loblolly pine site index first increased with low values of imbibitional water, reached a maximum at medium values, then finally decreased with high values of imbibitional water. Thus, the over-all relationship of subsoil moisture and aeration to pine site quality was established.

Turner (1938) made the only previous pine soil-site investigation in southern Arkansas. He concluded that site index for loblolly and shortleaf pines was most closely associated with slope percent, next with the textural composition of soil horizons as they affect internal drainage and aeration. He reported superior sites on flood plains of small streams. On uplands, the poorest sites were on soils of high clay content.

The Region

The region studied lies along the Arkansas-Louisiana state line, extending about 80 miles north into Arkansas and 30 miles south into Louisiana (Fig. 1). It is bordered on the east by the Mississippi and Arkansas River bottomlands, and on the west by the foothills of the Ouachita mountains and the Red River.

The climate is uniformly warm-temperate and humid. Precipitation averages about 50 inches. It is sometimes evenly distributed throughout the year, but severe summer droughts are common, and the autumn is characteristically dry. From 200 to 250 frost-free days may be expected per year.

The forest on uplands and stream terraces is a pine-hardwood mixture. Loblolly and shortleaf pine are the most important species, and are favored in forest management. In varying mixtures, other common species are southern red oak (*Quercus falcata* Michx.), sweetgum (*Liquidambar styraciflua* L.), and other upland hardwoods.

The Gulf Coastal Plain land surface was formed during several periods of sub-

mergence since Cretaceous time. Material carried down by regional drainage from the older mainland to the north was deposited as horizontal beds of clays and sands in the former shallow coastal waters. Successive uplifts exposed these marine beds, and erosion has long dissected and transfigured the terrain. From this land form have developed the gently rolling hills of the uplands and the flat terraces along major streams.

The soils belong to the great soils group known as Red and Yellow Podzolic. Upland soils are derived from the unconsolidated beds of sands and clays. Terrace soils are derived from old alluvium washed from

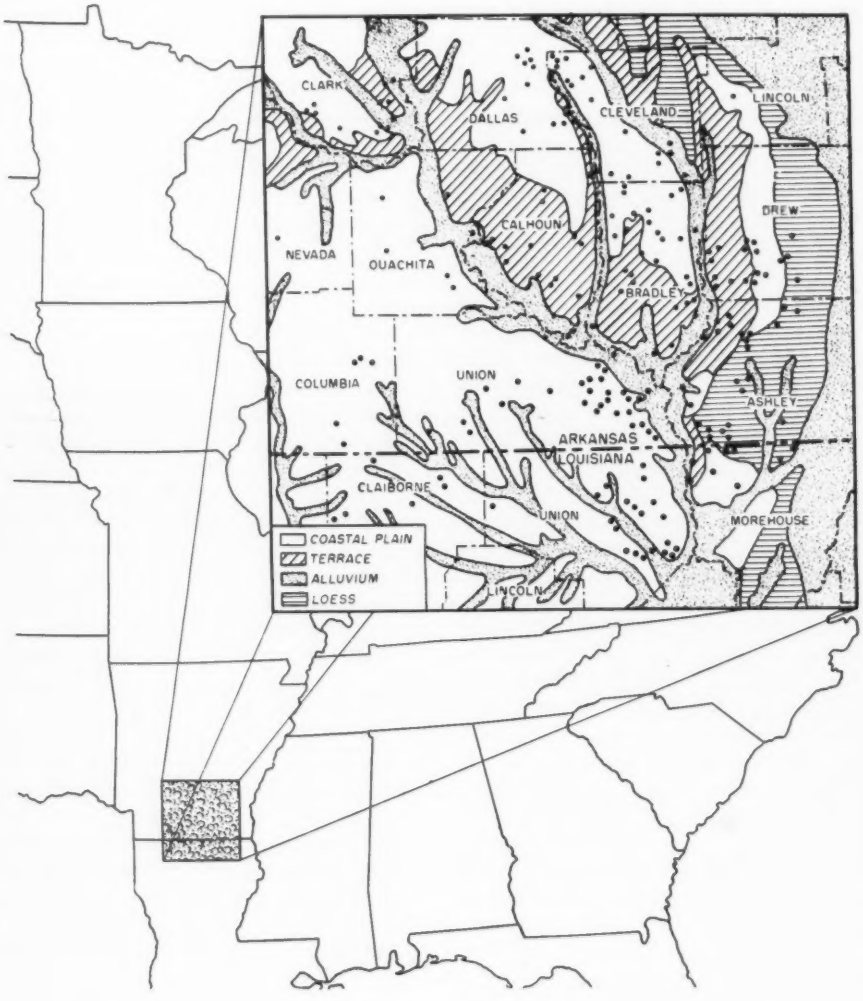

FIGURE 1. *Geologic provinces of the region studied, and location of sample plots.*

Coastal Plain and Ouachita uplands. All soils have developed in the warm, moist climate under the cover of pine-hardwood forest.

Soil profiles vary greatly. Subsoil texture may range from clay to sand, and internal drainage from poor to excessive. Surface soils are from a few inches to several feet thick. Horizons may be strikingly developed or nearly absent, the latter often a result of immature profile development on level areas.

Along the eastern edge of the study area lies a long, narrow belt of recent loess. Soils in this loess have not yet been correlated by the U. S. Department of Agriculture. It has not been determined whether the material is in its original wind-deposited state or was washed in from other areas. The uniform silt loam is underlain at 5 to 15 feet by alluvial sand and clay.

Collection of Data

Study plots were established in 38- to 60-year-old even-aged stands of loblolly and shortleaf pines, pure or mixed, which were judged by eye to maintain better than average stocking—75 to 100 square feet of basal area (Fig. 2). Site index was determined for a circular fifth-acre plot in each stand by adding 3 years to average age at breast height of 6 to 8 dominant and codominant trees and then referring to conventional site index curves (U. S. Forest Service, 1929). Soil profiles were described and soil samples taken from three post holes located systematically within the fifth-acre area and dug at least 48 inches deep.

A total of 206 plots were established in 16 counties of Arkansas and Louisiana from December 1953 to February 1955. Coastal Plain uplands were represented by 127 plots, stream terraces by 47 plots, bottomlands by 9, and the eastern loess by 23 (Fig. 1).

Of the 206 plots, 138 were in pure loblolly pine stands, 19 in pure shortleaf pine stands, and 49 in mixed stands. Site indices varied from 67 to 108 for loblolly pine, and from 63 to 93 for shortleaf pine. Table 1 shows the distribution of plots by age and site index classes.

Where loblolly and shortleaf pines occurred in mixed stands, loblolly was invariably the taller. The relationship of site index of loblolly pine to site index of shortleaf pine for the 49 plots in mixed stands was: Loblolly site index = 1.30 (shortleaf sites index) — 17.4. On poor sites shortleaf pine does nearly as well as loblolly, but as site index increases for both species, it increases in favor of loblolly pine. A site with an index of 95 for loblolly will have a shortleaf index of 86. This relationship agrees well with Coile's (1948) results in the Piedmont.

Eighty-five plots were in old-field stands. The remaining 121 were in areas which had never been cleared. Some of these latter stands were even-aged as a result of heavy logging or old burns, and some were

FIGURE 2. *One of the well-stocked, even-aged stands of loblolly-shortleaf pine typical of those sampled in this study.*

TABLE 1. Distribution of sample plots by age classes and site indices for loblolly and shortleaf pine.

Age class	Site index classes										Total
	61–65	66–70	71–75	76–80	81–85	86–90	91–95	96–100	101–105	106–110	
					LOBLOLLY PINE						
36–40	....	....	1	....	1	4	2	....	....	....	8
41–45	....	1	3	8	11	7	4	5	1	....	40
46–50	....	....	3	7	10	12	12	3	1	....	48
51–55	....	2	2	15	11	14	9	4	1	....	58
56–60	....	....	3	4	8	10	4	2	2	1	34
Total	....	3	12	34	41	47	31	14	5	1	188
					SHORTLEAF PINE						
36–40	1	....	....	....	1	1	....	....	....	....	3
41–45	....	1	3	7	1	....	....	....	....	....	12
46–50	1	....	4	3	4	1	1	....	....	....	14
51–55	....	....	4	9	5	1	....	....	....	....	19
56–60	....	4	5	4	5	1	1	....	....	....	20
Total	2	5	16	23	16	4	2	....	....	....	68

relatively even-aged portions of an all-aged stand condition.

All plots were classified as to topographic position and surface drainage. It was noted that site quality increased from ridges through terraces and flatwoods to bottoms. Or, as slope and surface drainage decreased, site index increased. Within each class, however, there was a wide spread of site indices.

Series names were assigned to each soil. Twenty-six different series were recognized, and these were represented by at least 57 different types.

The thickness of the surface soil, where readily discernible, was measured to the topmost subsoil layer, not necessarily to the least permeable horizon. A distinct change in color and texture, with a transition zone of not more than 3 inches between layers, was taken as the change from surface soil to subsoil. Where the transition zone was wide, no measurement was made.

Surface soil and subsoil samples were analyzed for total sand, silt, and clay content. The surface soil sample was from the horizon midpoint. The subsoil sample was from the heaviest and most plastic layer of the subsoil horizons, whether or not it immediately adjoined the surface soil. The moisture equivalent, wilting point, percent available water, and imbibitional water value were determined for these subsoil samples.

The pure loblolly pine and the loblolly component of the mixed loblolly-shortleaf pine plots were analyzed separately from the pure shortleaf pine and the shortleaf component of the mixed plots. Within each species group, secondary divisions of plots were desirable. It was decided that separation into geographic, geologic, or topographic groups would not be practical for the upland Coastal Plain and terrace soils, but plots on stream floodplains were separated.

Plots on the uncorrelated loess soils were also analyzed separately. The extent of this area is readily delineated geographically (Fig. 1), and the soils are characteristically different and easily recognized in the field.

Soils with readily distinguishable horizons, in which the surface soil thickness was measured, were classed as "zonal." Other soils, with poor differentiation of horizons, in which the surface layer blended gradually

over a wide transition into the subsoil, were classed as "azonal."[1] This zonal-azonal breakdown is useful and necessary for any practical field application of the results of this study (Zahner, 1957).

Three large groups of plots made up the bulk of the analyses (all on upland Coastal Plain and terrace soils):

Loblolly zonal, with 86 observations.
Loblolly azonal, with 69 observations.
Shortleaf zonal, with 56 observations.

In addition, there were four smaller groups:

Loblolly loess, with 23 observations.
Loblolly bottoms, with 9 observations.
Shortleaf azonal uplands, with 5 observations.
Shortleaf loess, with 7 observations.

The three large groups were each subject to detailed statistical analysis. The four smaller groups were analyzed less intensively, the last three only qualitatively.

Analysis of Large Groups

Soil and topographic characteristics for correlation with site index were chosen on the basis of other investigations and previous experience with the problem.

It seemed probable that the best relationships between site index and most of the site factors would not be simple linear ones. Curvilinear trends were therefore investigated before regression analysis was begun. This was done with scatter diagrams. Site index was plotted over each site factor for all observations within a group, and the trend of mean site indices noted.

Several factors showed no apparent trend. For the loblolly and shortleaf zonal groups these factors were the percent sand, silt, or clay in the surface soil, percent available water in the subsoil, percent silt in the subsoil, and aspect. For the loblolly azonal group no trends could be identified for percent clay in the surface soil, percent available water in the subsoil, and aspect. Moisture equivalent and wilting point of the subsoil showed only slight or doubtful trends in all groups. All these variables were eliminated from further analysis.

For the loblolly and shortleaf zonal groups, the following trends were strong, and appeared to have definite effects on site index: (1) imbibitional water value of the subsoil, (2) percent clay in the subsoil, (3) percent silt-plus-clay in the subsoil, (4) thickness of the surface soil, and (5) slope.

For the loblolly azonal group, these trends were strong: (1) percent silt in the surface soil, (2) imbibitional water value of the subsoil, (3) percent clay in the subsoil, (4) percent silt in the subsoil, (5) percent silt-plus-clay in the subsoil, and (6) slope.

Individual multiple regressions were prepared for each of the three large groups of plots. Eighteen independent variables, representing various functions of the soil and topographic data, were tested for the loblolly zonal group, 15 variables were tested for the loblolly azonal group, and 9 for the shortleaf zonal group.

When a single site factor was represented by more than one variable (as thickness of surface soil, for example, was represented by both linear and curvilinear functions), all variables representing that factor were fixed in the analysis one after another, before additional factors were tested. Sometimes several variables were needed to express the full effect of a factor even though any one alone contributed very little, while in other cases one variable alone made the full contribution.

Loblolly zonal group (86 plots). It was found that subsoil clay content had approximately the same effect as did subsoil imbibitional water, but that one factor rather completely nullified the effect of the other. This result was expected, because of the close correlation between the two.

Further analysis tested four possible in-

[1]The terms "zonal" and "azonal" are employed for convenience, although some of the "azonal" soils in this study are not truly azonal according to strict classification. The "azonal" profiles of this study have "gradual" or "diffuse" boundaries between horizons as defined on page 187 of the Soil Survey Manual (U. S. Dept. Agr. Handbook 18). No distortion of established technical terms is intended.

teractions between thickness of surface soil and the two subsoil factors, but all failed to show significance.

The relationship between site index and the clay content of the subsoil appeared from preliminary plotting to require a third-power curvilinear function. A test showed this cubic function to be highly significant. A subsequent test for imbibitional water value failed to improve the regression significantly. The clay content then accounted for substantially more of the site index variation than did the imbibitional water value.

Preliminary plotting had also indicated the possibility of reciprocal functions for the effect of the thickness of surface soil and the effect of slope. However, a quadratic function gave the best fit for surface soil thickness, while a simple linear function satisfactorily accounted for the effect of slope. Interactions between slope and surface soil thickness and between slope and subsoil clay showed no significance when variations attributable to main effects were accounted for.

Other variables tested in this group had no significant effect on site index.

Loblolly azonal group (69 plots). It was known that several of the subsoil factors tested in this group were closely associated with one another, and that one would nullify the others when tested for contributions to residuals of site index. Either the silt-plus-clay or sand content, in quadratic form, contributed the largest effect. Clay content and silt content alone were therefore discarded, as was imbibitional water.

Silt content of the surface soil was found to be a significant factor. Tests of joint effects, moreover, showed that surface soil silt had a greater correlation with site index in conjunction with either subsoil silt-plus-clay or sand content than it did independently.

A linear combination of percent slope with its reciprocal was found to be the best expression for this topographic variable. (Each slope was coded by being increased by 0.1 percent, to avoid an infinite reciprocal.) Other forms of topographic variables were not significantly correlated with site index.

Shortleaf zonal group (56 plots). Preliminary diagrams indicated that this group was affected by essentially the same site factors as the loblolly zonal group. It was thought desirable to keep the two groups comparable so that similar site factors could be related to site index for the two species.

In this group, the cubic function of subsoil clay content was not significantly related to site index. For percent slope, a quadratic function proved significant. Otherwise, the same site variables prevailed as for zonal loblolly. No joint relationships among surface soil thickness, subsoil clay content, or slope were found significant.

Regression equations. In all three groups both a coded logarithmic and the uncoded form of site index were tested. The uncoded forms gave slightly better correlation coefficients than did the logarithmic forms.

Three regressions for estimating site index were developed.

Loblolly pine on upland zonal soils:

$$\text{Site Index} = 33.58 + 3.174(Cl) - 0.0827\ (Cl^2) + 0.00063\ (Cl^3) + 2.257\ (T) - 0.0615\ (T^2) - 0.739\ (Sl).$$

Loblolly pine on upland azonal soils:

$$\text{Site Index} = 69.51 + 1.805\ (Sa) - 0.0215\ (Sa^2) - 2.77\ (Sl + 0.1) - 1.227/(Sl + 0.1) - 0.0062\ (Sa)\ (Si)$$

Shortleaf pine on upland zonal soils:

$$\text{Site Index} = 58.53 + 1.618\ (T) - 0.0419\ (T^2) + 0.852\ (Cl) - 0.0121\ (Cl^2) - 2.64\ (Sl) + 0.117\ (Sl^2).$$

T = thickness of surface soil, in inches
Cl = percent clay of subsoil
Sa = percent sand of subsoil (or 100 minus percent silt-plus-clay of subsoil).
Si = percent silt of surface soil
Sl = percent slope

Multiple correlation coefficients for the

three regressions are 0.772, 0.839, and 0.868. The analyses of variance and the standard errors of the regression coefficients are given in tables 2 and 3.

The standard errors of the regression estimates shown in table 3 were well below the standard deviations of the site indices about their respective means, both of which are shown below:

Loblolly zonal mean site index = 84.00 feet ± 6.82

Loblolly azonal mean site index = 85.04 feet ± 6.26

Shortleaf zonal mean site index = 75.70 feet ± 5.71

Results for Large Groups

The results of the analyses of the three large groups of plots can best be summarized by graphs showing calculated relationships between site variables and site index. The data are limited to the range of field observations in each group, as no extrapolation has been attempted.

Loblolly zonal. The regression analysis for this group shows close correlation between site index and thickness of surface soil, clay content of subsoil, and percent slope (Fig. 3). Site index is seen to increase with thickness of surface soil to a maximum at about 18 inches. It then levels off and begins to decrease.

Clay content of the subsoil affects site index strongly as it increases from sands to clay loams. Site index reaches a maximum at a clay content of about 25 percent, then begins to decrease sharply as clay increases to 60 percent. Clay content beyond 60 percent apparently has little effect on site.

Increasing slope results in a decreasing site index. The relationship is linear from a 1-percent slope up to about 12 percent. Perfectly level areas of zero slope and steep slopes of more than 15 percent were not encountered in the sample of this group.

For the range in observations, thickness of surface soil alone affects site index by a maximum of 17 feet, clay content of subsoil affects it by 13 feet, and slope by 10 feet. The maximum change in regression

TABLE 2. Analysis of variance for regressions of the three large groups of plots.

Source of variation	Degrees of freedom	Mean square
Loblolly zonal group (86 plots)		
(1) Percent clay of subsoil	3	458.6**
(2) Thickness of surface soil (1 fixed)	2	388.2**
(3) Percent slope (1 and 2 fixed)	1	199.1**
Residuals	79	20.21
Loblolly azonal group (69 plots)		
(1) Percent sand of subsoil	2	389.9**
(2) Percent slope (1 fixed)	2	459.1**
(3) Product of percent silt of surface soil times percent sand of subsoil (1 and 2 fixed)	1	177.3**
Residuals	63	12.50
Shortleaf zonal group (56 plots)		
(1) Thickness of the surface soil	2	289.3**
(2) Percent clay of subsoil (1 fixed)	2	134.7**
(3) Percent slope (1 and 2 fixed)	2	252.8**
Residuals	49	9.01

**Significant at 1-percent level.

TABLE 3. Standard error of estimate along with regression coefficients and their standard errors.

LOBLOLLY ZONAL GROUP (79 D.F.)[1]	
Error of estimate	±4.50
Subsoil clay	3.174±0.729
(Subsoil clay)^2	−0.0827±0.0194
(Subsoil clay)^3	0.00063±0.00016
Surface soil thickness	2.257±0.397
(Surface soil thickness)^2	−0.0615±0.0118
Slope	−0.739±0.236
LOBLOLLY AZONAL GROUP (63 D.F.)	
Error of estimate	±3.54
Subsoil sand	1.805±0.265
(Subsoil sand)^2	−0.0215±0.0031
Slope + 0.1	−2.770±0.442
1/(slope + 0.1)	−1.227±0.176
(Subsoil sand) × (surface soil silt)	−0.0062±0.0016
SHORTLEAF ZONAL GROUP (49 D.F.)	
Error of estimate	±3.00
Surface soil thickness	1.618±0.342
(Surface soil thickness)^2	−0.0419±0.0096
Subsoil clay	0.852±0.201
(Subsoil clay)^2	−0.0121±0.0028
Slope	−2.64±0.52
(Slope)^2	0.117±0.036

[1]d.f. = degrees of freedom.

surface from the worst combination (shallow surface soil, heavy clay subsoil, and steep slope) to the most favorable (moderately deep surface soil, sandy clay loam subsoil, and flatwoods topography) varies from a site index of about 60 to one over 90—a spread of 30 feet. Field observations ranged up to site index 104, and several plots had indices above the highest obtainable by the equation.

Loblolly azonal. The regression analysis for this group shows that site index is correlated with the silt content of the surface soil, the silt-plus-clay content of the subsoil, and slope (Fig. 4). Site index decreases with increasing percent silt of the surface soil. This effect is not so great with subsoils of high silt-plus-clay content as with those of low silt-plus-clay. This interaction is clearly demonstrated in the figure.

Site index increases with increasing silt-plus-clay of the subsoil to a maximum at 60 percent silt-plus-clay (where surface soil silt is 20 percent). Site index then decreases with further increases in silt-plus-clay. Optimum silt-plus-clay varies as the silt content of the surface soil changes.

Slope has an interesting effect on site index. A site of 0 slope is poorer than a site of 1 percent. Then as slope increases beyond 1 percent, site index decreases gradually. In this group, slopes of more than 5 percent were not encountered in the field.

For the range of observations, surface soil silt alone affects site index by a maximum of about 5 feet (for moderate ranges of subsoil silt-plus-clay), silt-plus-clay of the subsoil affects site index by 13 feet, and slope by 8 feet. The maximum change in regression surface from the worst combination (high surface soil silt content, heavy

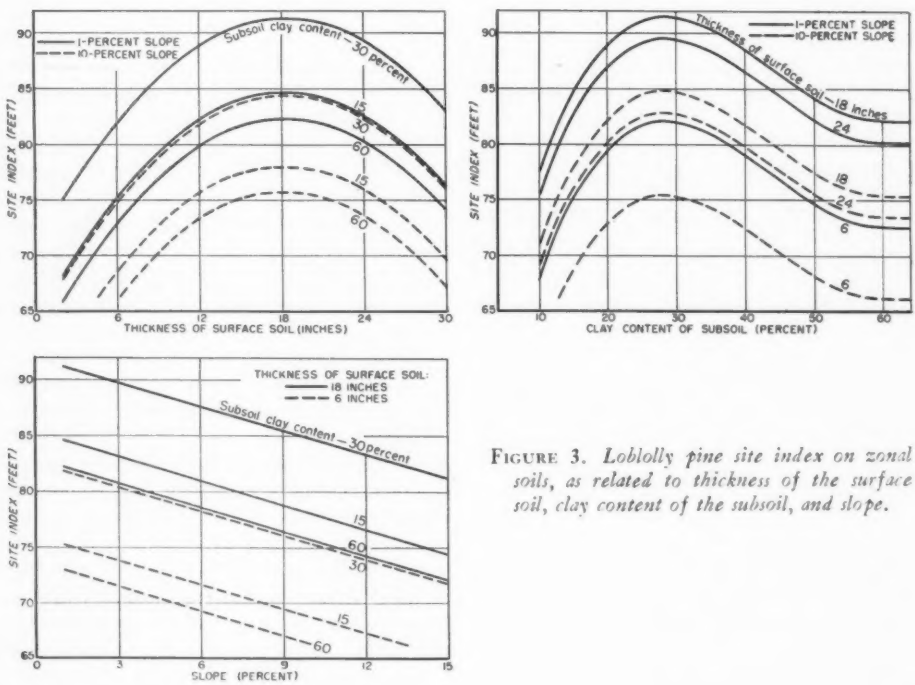

FIGURE 3. *Loblolly pine site index on zonal soils, as related to thickness of the surface soil, clay content of the subsoil, and slope.*

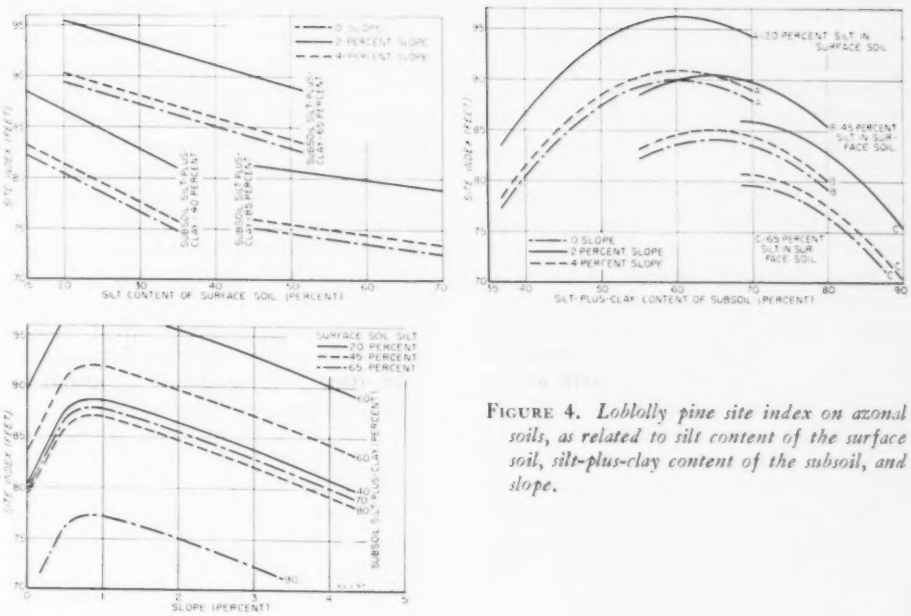
0 SLOPE
2 PERCENT SLOPE
4 PERCENT SLOPE
SITE INDEX (FEET)
SILT CONTENT OF SURFACE SOIL (PERCENT)
SUBSOIL SILT PLUS CLAY 40 PERCENT
SUBSOIL SILT PLUS CLAY 60 PERCENT
SUBSOIL SILT PLUS CLAY 80 PERCENT
20 PERCENT SILT IN SURFACE SOIL
45 PERCENT SILT IN SURFACE SOIL
65 PERCENT SILT IN SURFACE SOIL
SILT-PLUS-CLAY CONTENT OF SUBSOIL (PERCENT)
SURFACE SOIL SILT
20 PERCENT
45 PERCENT
65 PERCENT
SUBSOIL SILT PLUS CLAY PERCENT
SLOPE (PERCENT)

FIGURE 4. *Loblolly pine site index on azonal soils, as related to silt content of the surface soil, silt-plus-clay content of the subsoil, and slope.*

silty clay subsoil, and either 0- or 4-percent slope) to the most favorable (sandy loam surface soil, clay loam subsoil, and 1- to 2-percent slope) is the difference between a site index of 75 and one of 97. This change is not quite so great as that exhibited by the regression surface of the zonal loblolly. Several sample plots lie above and below the maximum and minimum regression surface, however.

Shortleaf zonal group. The regression analysis shows that the same three factors which affect loblolly pine on zonal soils also affect shortleaf pine.

Site index increases with increasing thickness of the surface soil to a maximum, then decreases with further increases in surface soil thickness (Fig. 5). The maximum site index is reached at the same soil thickness for both species—about 18 inches.

Site index increases with increasing clay content to a maximum, then decreases. Maximum site index is reached at a higher clay content than for loblolly, 35 percent versus 25 percent. The slope of the site curve is somewhat less steep for shortleaf, as the same increment of subsoil clay does not mean an equal increment of site index for the two species. The shortleaf curve does not indicate a tendency to level off at high values of clay content, as does the loblolly curve.

Slope presents a definite curvilinear relationship with site index. As slope increases from 1 to 5 percent, site index decreases rapidly. Then as slope approaches 10 percent, its effect on site index levels off. Only 1 shortleaf plot had slope exceeding 12 percent, and no plots of 0 slope were encountered.

For the range of observations, thickness of surface soil alone affects site index by a maximum of 10 feet, subsoil clay by 8 feet, and percent slope by 12 feet. The maximum change in regression surface from the

worst combination (shallow surface soil, sandy loam or heavy clay subsoil, and steep slope) to the best combination (moderately deep surface soil, clay loam subsoil, and flatwoods topography) is the difference between a site index of 60 and one of 87.

Errors of estimate. Multiple correlation coefficients are highly significant and show excellent correlation for all groups. Two common sources of error were kept to a minimum: ages of stands used in the field sample were restricted to the range 38–60 years so that estimates of site index at age 50 years were accurate; and the region studied is relatively small, with a uniform climate and a single geologic history.

The high shortleaf correlation can be partly explained by the natural occurrence of this species in the field. Although found on all topographic positions, it occurs in stands which are homogeneous or only slightly sprinkled with loblolly, principally on inferior sites such as ridges and upper slopes. Most of the shortleaf plot observations were in a compact five-county region in south-central Arkansas. The restricted geographic distribution, combined with the limited topographic observations, contributed to the high correlation coefficient in this group.

Loblolly pine, on the other hand, was found uniformly distributed in all situations. The heterogeneity of site conditions and the wide geographic pattern of distribution may be partly responsible for the somewhat poorer correlations for loblolly.

A separate and independent field test was made of the three prediction equations. Plots were established in 21 additional stands of pine similar to the 206 used in the original field sample. Nine were in loblolly pine on zonal soils, 7 in loblolly pine on azonal soils, and 5 in shortleaf pine on

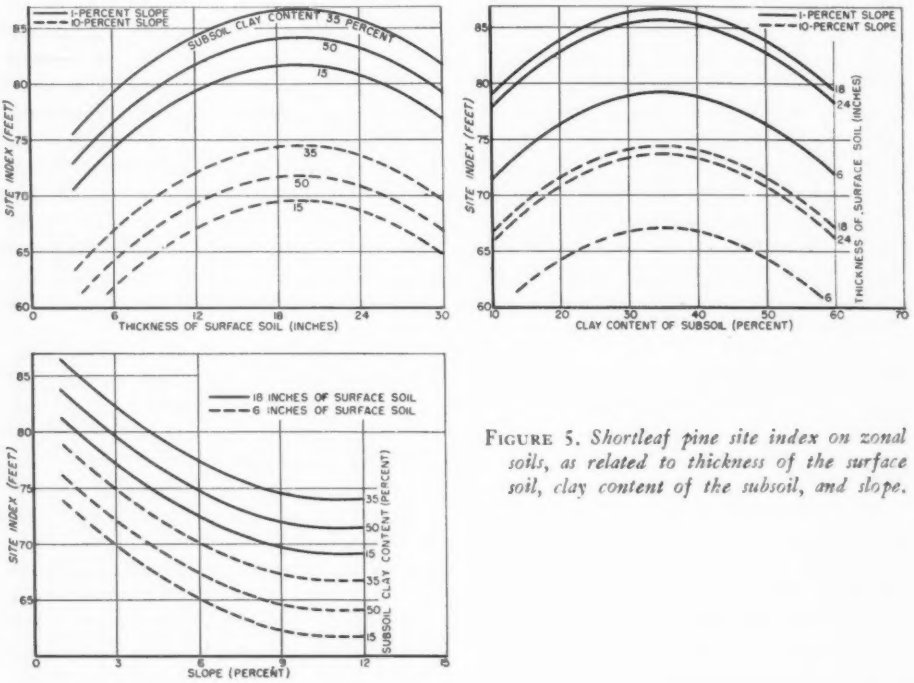

FIGURE 5. *Shortleaf pine site index on zonal soils, as related to thickness of the surface soil, clay content of the subsoil, and slope.*

zonal soils. Estimates were made for the site index of each plot from the appropriate equation and then compared with the site index measured from trees.

The calculated estimates were within 10 percent of the measured for all 21 test plots. The average departure of estimated from measured site index was about 4 percent.

Analysis and Results of Small Groups

Loblolly loess. Soil and topography found on this parent material have a uniformity not known in the Coastal Plain and terrace uplands of the rest of the study area. Site quality is good to excellent, the average index for loblolly pine being 92 for the 23 observations. The bulk of the observations fell in the 10-foot range from 85 to 95—a testimony to the uniformity of conditions.

In scatter diagrams none of the measured soil and topographic variables showed any consistent trends with site index. Regression analysis confirmed this.

The regression analysis tested all of the independent variables tested originally in the loblolly azonal group, and additional joint variables involving surface and subsoil texture as well as several soil-moisture properties — moisture equivalent, wilting point, and available water. None of these site factors showed significance.

The soils in this group were finally classified by internal drainage. The poorly drained class, represented by only 4 observations, showed a consistently lower site index than the imperfectly to well-drained class, with 19 observations. The mean site index of those soils in the latter class is about 95, with most sites falling in the range 90 to 100. The less important poorly drained soils appear to have sites in the range 80 to 90.

Loblolly bottomland. The 9 observations in this group were useful only for two generalized comparisons: (1) The average site index of the bottomland plots was found to be considerably higher than that for the uplands (with the exception of the loess group). The range in site index was small compared to the upland groups, varying from 87 to 102, with an average of 94. (2) Within the group itself, it was noted that the average site index of 4 plots on large stream floodplains was 92, and that of 5 plots on small stream floodplains was 97. The difference between the two categories was consistent.

Shortleaf azonal uplands and loess. These groups contained only a small percent of all the shortleaf plots on upland Coastal Plain and terrace soils and on loess soils. Eleven of the 12 plots were in mixed loblolly-shortleaf stands, with loblolly pine the predominant species. No soil-site trends were noted.

On these loessial and azonal soils, shortleaf site index, like that of loblolly, averaged considerably better than that on zonal soils. The range in site index on loess plots was not large, from 80 to 88, again attesting to the uniformity of these sites.

Discussion

Surface soil properties. In the zonal group, the depth of the surface soil is a measure of the soil available for occupancy by small roots. The sandy loam surface generally found in this group is a well-aerated environment for roots. As discussed earlier, many investigators have shown that the depth of surface soil influences site index for the southern pines, especially for loblolly and shortleaf. This study uncovered a relationship that has not been reported previously. That is, when the surface horizon is so deep that it in effect becomes a lower horizon, other properties than its mere thickness probably are important. Evidently surface soils 18 inches thick provide adequate growing space for small roots. Greater thicknesses are not used by small roots, and that part of the surface soil below 18 inches has the effect of a subsoil. As will be discussed later, sandy loam subsoils do not have desirable moisture properties for good growth, and thus affect site adversely. So it is with light-textured deep surface soils below 18 inches. For example,

a 28-inch surface soil may not be so good as a 16-inch soil, because its lower depths may lack the water-holding capacity of a finer-textured subsoil under the shallower surface soil.

Where profiles are well developed (zonal), surface soils vary but little in texture. Sandy loams predominate. There is thus little difference in the quality of this surface laver from one site to another. The azonal loblolly pine group presents a different relationship. Other factors being equal, increases in silt content reflect decreases in soil porosity and poorer soil aeration. Soils in this group are immature. Some profile development has occurred, but there are still close relationships between the various horizons.

Poorly aerated subsoils are accompanied by poorly aerated surface soils. In other words, surface soils with very high silt content overlie subsoils with high silt-plus-clay content. Naturally, when subsoils are poorly aerated and already limit growth, the effect of decreasing surface soil aeration may not be so noticeable per unit of decrease as when subsoils are more favorable to growth. Thus the poorly aerated subsoil accounts for most of the lowering of site index in such soils, and the joint effect of surface soil silt is less important.

Subsoil properties. This study demonstrates directly the curvilinear relationship between subsoil texture and site index. The indirect method of working through imbibitional water values was found unnecessary. Imbibed water is closely related to the type of clay mineral as well as the content of clay present. Most soils in the area studied are probably low in montmorillonite–type minerals—which imbibe large quantities of water—while some soils in other regions of the South contain a higher proportion of this type of clay.

On zonal soils, total clay content resulted in a better statistical fit of the data than did imbibitional water. The explanation of the changing effect on site index by increasing clay content is almost identical to that already reported for increasing imbibitional water (Zahner, 1954). An increase in clay from 10 to 25 percent represents improvement in soil moisture conditions. As the subsoil changes from sands to light clays, site quality increases accordingly. As clay content reaches 25 percent for loblolly pine (35 percent for shortleaf), however, soil aeration may become a limiting factor even though moisture conditions may continue to improve. Site index then may decrease with increasingly poorer aeration, up to a clay content of 60 percent.

In the azonal soils, silt-plus-clay content presents a better measure of moisture and aeration than does either the clay content alone or imbibitional water. Here the silt fraction is the most important textural component. Silt content alone of subsoils in this group averaged 45 percent, 15 percent higher than in the zonal group. Silt-plus-clay contents were about the same for the two groups, averaging 63 percent in the zonal and 64 percent in the azonal group—an indication that the clay fraction does not play as important a part in the latter group.

Topography. In the rolling hills of southern Arkansas and northern Louisiana, well-developed zonal soil profiles are the general rule. The azonal, poorly differentiated horizons are more limited to upland flatwoods and terraces. Both the zonal and the azonal conditions are equally important in terms of the forest area they represent.

Ridges and upper slopes are, of course, drier and generally poorer sites than gentle slopes and terraces. On zonal soils, both species attain by far their best growth on more level areas. It should be noted that loblollly pine site index decreases steadily as slope increases, but that shortleaf site index decreases at a diminishing rate.

In the azonal group the total range in slopes was only from 0 to 5 percent. A 0 slope (no measurable surface drainage) was found to be no better site for loblolly pine than a well-drained, 4-percent slope. Sites with just adequate drainage—1- and

2-percent slope—are the best. Evidently soil aeration is limiting to growth on the extremely flat areas.

The flood plains of large streams, as the Ouachita River, contain much flat, poorly drained soil. Pine has not been found in these areas in stands suitable for sampling, but poor soil aeration, together with poor hardwood timber growth, indicates that the sites are not good. Lesser drainages and small stream bottoms, on the other hand, are characterized by moderate to good internal drainage, and should have a loblolly site index of 95 to 100.

Soil aeration. Poor soil aeration in itself may or may not be directly responsible for poor site quality. Usually, low aeration is associated with high soil moisture in the soils studied. In a tight clay or slowly permeable silty clay loam, for example, water storage is often greater than in well-aerated soils.

Indirectly, however, poor aeration is probably responsible for moisture deficiencies. When soil dries somewhat through evapo-transpiration, the sparsely developed root system in a poorly aerated soil suffers from moisture deficiency even though the soil as a whole may not be dry, for roots must be in contact with water before they can absorb it. During dry periods, which occur nearly every growing season in the Midsouth, trees on poorly aerated soil may suffer more than those on better aerated soil, simply because their root systems have not permeated the soil sufficiently to take advantage of all the stored water.

The above discussion is not to be taken as dismissing the direct effects of poor soil aeration. Pine growth may also be limited by reduced metabolic activities in the roots and by reduced absorption of water and minerals—the results of the low oxygen and high carbon dioxide environment in poorly aerated soil.

Summary

Site characteristics and site index were measured in 206 even-aged stands of loblolly and shortleaf pines in southern Arkansas and northern Louisiana. Through regression analysis site index was related to soil and topographic variables. Site factors that help regulate soil moisture and soil aeration were highly correlated with site index. Areas studied had site indices (at age 50 years) ranging from 67 to 108 for loblolly pine, and from 63 to 93 for shortleaf pine.

On mature upland soils with well-differentiated horizons, both loblolly and shortleaf pines are influenced similarly: (1) As the thickness of surface soil increases, site index also increases, but only to a soil depth of about 18 inches. Site index then levels off, and finally decreases somewhat for still deeper surface soils. (2) As the clay content of the subsoil increases from 10 to 25 percent for loblolly pine, and from 10 to 35 percent for shortleaf pine, site quality first increases and then levels off. There is a final decrease in site quality for the higher values of clay content. (3) Site index decreases with increases of slope.

On immature soils with poor horizon development, loblolly pine site index is associated with three factors: (1) As the silt content of the surface soil increases, site quality was found to decrease. The effect of surface silt is greater for those soils with low subsoil silt-plus-clay content than for those with high subsoil silt-plus-clay content. (2) As the silt-plus-clay content of the subsoil increases from 35 to 65 percent, site quality first increases and then levels off. For higher values of silt-plus-clay, site index decreases. (3) Site index is better on areas with just adequate surface drainage than on flat areas with no drainage or on slopes with good drainage. Shortleaf pine does not usually occur in high proportion with loblolly pine on azonal soils.

In general, it was concluded that the best sites for loblolly pine in the region studied are the better drained small stream bottoms. Next, loblolly and shortleaf pines both grow well on the better drained loess, upland terrace, and flatwoods soils. The upper slopes and ridges generally are poorer

sites. In all topographic positions, the best sites are those of moderately deep sandy loam surface soils with clay loam subsoils. Poorest sites are shallow surface soils overlying heavy clay subsoils, or deep sandy surface soils overlying sandy subsoils. Extremely flat soils of high silt and clay content, with no surface or internal drainage, are also relatively poor.

Literature Cited

BARNES, R. L., and C. W. RALSTON. 1955. Soil factors related to growth and yield of slash pine plantations. Fla. Agric. Expt. Sta. Bull. 559. 23 pp., illus.

BILLINGS, W. D. 1952. The environmental complex in relation to plant growth and distribution. Quart. Rev. Biol. 27: 251-265, illus.

COILE, T. S. 1935. Relation of site index for shortleaf pine to certain physical properties of the soil. J. For. 33: 726-730, illus.

———. 1948. Relation of soil characteristics to site index of loblolly and shortleaf pines in the lower Piedmont region of North Carolina. Duke Sch. For. Bull. 13. 78 pp., illus.

———. 1952. Soil and the growth of forests. Advances in Agron. 4: 329-398, illus.

———, and F. X. SCHUMACHER. 1953. Relation of soil properties to site index of loblolly and shortleaf pines in the Piedmont region of the Carolinas, Georgia, and Alabama. J. For. 51: 739-744, illus.

DINGLE, R. W. and P. Y. BURNS. 1954. Relationship of shortleaf pine growth to soil properties. Mo. Agric. Expt. Sta. Res. Bull. 541. 11 pp., illus.

GAISER, R. N. 1950. Relation between soil characteristics and site index of loblolly pine in the Coastal Plain region of Virginia and the Carolinas. J. For. 48: 271-275, illus.

———. 1951. Relation between topography, soil characteristics, and the site index of white oak in southeastern Ohio. U. S. For. Serv. Central States For. Expt. Sta. Tech. Pap. 121. 12 pp., illus.

GOGGINS, J. F. 1951. Slash and loblolly pine plantations in Alabama's Piedmont region. Ala. Agric. Expt. Sta. Cir. 99. 22 pp., illus.

HEIBERG, S. O., and D. P. WHITE. 1956. A site evaluation concept. J. For. 54: 7-10.

MCCLURKIN, D. C. 1953. Soil and climatic factors related to the growth of longleaf pine. U. S. For. Serv. South. For. Expt. Sta. Occas. Pap. 132. 12 pp., illus.

METZ, L. J. 1950. Relationship between soil properties and the growth of loblolly pine in the Southeastern Coastal Plain. Unpub. thesis, Duke Univ. 51 pp., illus.

RALSTON, C. W. 1951. Some factors related to the growth of longleaf pine in the Atlantic Coastal Plain. J. For. 49: 408-412, illus.

TURNER, L. M. 1938. Some profile characteristics of the pine-growing soils of the Coastal Plain region of Arkansas. Ark. Agric. Expt. Sta. Bull. 361. 52 pp., illus.

U. S. FOREST SERVICE. 1929. Volume, yield, and stand tables for second-growth southern pines. U. S. Dept. Agric. Misc. Publ. 50. 202 pp., illus.

ZAHNER, R. 1954. Estimating loblolly pine sites in the Gulf Coastal Plain. J. For. 52: 448-449.

———. 1957. Field Procedures for soil-site classification of pine land in south Arkansas and north Louisiana. South. Forest Expt. Sta. Occas. Paper 155. 17 pp. illus.

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